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The Octandrous and Dodecandrous Species of *Topobea* (Melastomataceae) in Mexico and Central America

by

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A regional revision of the octandrous and dodecandrous species of *Topobea* is presented that recognizes 24 species in Mexico and Central America. This summary includes a key, descriptions, distributional and phenological information, discussions of useful taxonomic characters, and a brief review of what is known about the reproductive biology of *Topobea*. Rationale is given for placing nine species in synonymy. Illustrations are provided for four new species (*T. amplifolia*, *T. dimorphophylla*, and *T. gerardoana* from Costa Rica; *T. tetramera* from Panama), and for *T. multiflora*, a species erroneously reported for Costa Rica as *T. calycularis*. Representative specimens are cited to document the geographic distribution and range of variability for each species.

RESUMEN

Se presenta una revisión de las 24 especies de *Topobea* en México y América Central que tienen ocho y doce estambres. Este resumen incluye una clave, descripciones, información sobre distribución y fenología, y discusiones de caracteres taxonómicos muy útiles en *Topobea*. También se presentan ilustraciones para cuatro especies nuevas (*T. amplifolia*, *T. dimorphophylla*, y *T. gerardoana* de Costa Rica; *T. tetramera* de Panamá), y para *T. multiflora*, una especie erróneamente reportada para Costa Rica como *T. calycularis*. Especímenes representativos son citados para documentar la distribución geográfica y el rango de variabilidad de cada especie.

Topobea, with approximately 70 species, is one of two genera comprising the neotropical tribe Blakeeae. This tribe is readily recognized by its prevailing 6-merous axillary flowers that are individually subtended by two pairs of decussate bracts, baccate fruits, and ovoid to pyramidal seeds with a smooth testa (Almeda 1990).

Most species of *Topobea* are shrubby epiphytes of wet forest habitats; some are terrestrial shrubs, and a few attain arborescent dimensions. More than 75% of the species occur in a narrow equatorial band centered in Colombia, ranging south to Ecuador and north to Costa Rica. Another dozen or so species extend north to southern Mexico and south to Bolivia and Brazil. Because of their showy flowers, the terrestrial species, some of which are locally common, have been collected with increasing frequency in recent decades. Because so many species of *Topobea* are obligate epiphytes with very local distributions, newly discovered species have come to light with increasing frequency as the forest canopies of tropical America have received increased exploratory attention in the last two decades.

Topobea was last treated in its entirety by Cogniaux (1891) who recognized 24 species, five of which were reported for the Mesoamerican region. Subsequent regional floras (Gleason 1958; Standley 1924, 1938; Standley and Williams 1963; Winkler 1965) collectively attributed 17 species of

Topobea to Mexico and Central America, only six of which are recognized here as distinct taxa. This study of the octandrous and dodecandrous species of Mexico and Central America and my recent revision of the Central American hexandrous clade (Almeda 2000a) recognize a total of 29 species of *Topobea* for the region. Including the four new species proposed here, over half of these have been described or transferred to *Topobea* in the last 17 years.

TAXONOMIC TREATMENT

***Topobea* Aubl., Hist. Pl. Guiane Fr. 1:476. 1775.**

TYPE: *Topobea parasitica* Aubl.

Trees, shrubs, or woody vines, often epiphytic with glabrous or variously pubescent terete to quadrate branchlets. Leaves coriaceous or chartaceous, 3–7-nerved or plinerved, often with the transverse secondary veins closely spaced, straight and parallel. Flowers 6-merous (rarely 4-merous), diplostemonous (haplostemonous in five Mesoamerican species), axillary, solitary or fascicled, typically pedunculate in the upper leaf axils and subtended by two pairs of decussate, free or partially fused, coriaceous or foliaceous bracts inserted at the base of the hypanthium. Hypanthium campanulate or suburceolate; calyx persistent, truncate or 6-lobate (4-lobate in one species). Petals white or pink, magenta or some combination of these colors, glabrous to sparsely pubescent abaxially, sometimes ciliolate at the margins. Stamens 12 or 6 (8 in one species), isomorphic and glabrous; anthers linear-oblong or subulate, uniporose or biporose with 2 dorsally-inclined apical pores that are approximate, cleft and divergent, or often confluent at anthesis; connective simple and unappendaged or thickened and modified basally at or near the filament insertion into a spur or caudiform appendage. Stigma punctiform to capitate. Ovary completely or partly inferior but varying to superior in a few species, usually 6-locular (consistently 2- or 4-locular in some species). Fruit baccate; seeds clavate to cuneate or narrowly pyriform.

Until recently, the tribe Blakeaceae was thought to be constant with respect to ovary position and number of perianth parts and ovary locules (Almeda 1990, 2000a). Descriptive literature on the tribe describes it as having 6-merous flowers with 12 stamens (dodecandrous) and a 6-locular inferior ovary (Almeda 1990). This characterization still holds true for *Blakea*, which is distinguished from *Topobea* by its laterally compressed anthers that are biporose, oval, oblong, or elliptic and obtuse to rounded apically with 2 well-separated (and typically minute) apical pores (Almeda 2000b). *Topobea*, on the other hand has uniporose or biporose anthers that are linear-oblong to oblong-subulate (usually not compressed laterally) with dorsally-inclined apical pores that are commonly confluent or cleft and divergent. Most species of *Topobea* are similar to *Blakea* in having 6-merous flowers that are dodecandrous and a 6-locular ovary. This appears to be the plesiomorphic condition in the tribe. Critical study of the Mesoamerican species of *Topobea* reveals that only five species have completely inferior ovaries and a surprising number exhibit an evolutionary reduction series involving stamen and ovary locule number. The species of *Topobea* treated here fall into three groups based on stamen number. The most extraordinary one in this regard is *T. tetramera*. As its specific epithet implies it has 4-merous flowers that are octandrous (with eight stamens) and its ovary is inferior and 4-locular. The second, a highly derived group of five species, is characterized by 6-merous flowers that are hexandrous (with 6 stamens) and an inferior ovary that is either 2- or 4-locular (Almeda 2000a). The third group consists of the remaining 23 dodecandrous species. Seventeen of these have a 6-locular ovary, five are consistently 4-locular, and one, *T. albertieae*, is prevalingly 4-locular with the occasional 3- or 5-locular ovary. Reduction in stamen number is consistently correlated with an inferior ovary position in the hexandrous and octandrous species. This kind of character correlation, however, breaks down among the dodecandrous species. The following



PLATE 1. *Topobea fragrantissima* Almeda. Original gouache and acrylic on hotpress illustration board by Meg Stalcup in July, 2001.

examples serve to illustrate this point: *T. aeruginosa* has 6:12:6 (petals: stamens: locules) with a completely inferior ovary; *T. brenesii* also has 6:12:6 but its ovary is wholly superior; *T. watsonii* with 6:12:6 has an ovary that is 1/3-inferior; *T. dodsonorum* has 6:12:4 and a 1/2-inferior ovary; *T. pittieri* has 6:12:4 and a 3/4-inferior. Among the dodecandrous species, the lack of correlation between ovary position and locule number provides information for identifying phenetic gaps and useful character combinations for species delimitation. It provides a challenge, however, when attempting to determine derived character states for phylogenetic reconstruction. The general assumption among students of the Melastomataceae has been that a superior ovary is plesiomorphic and an inferior ovary is apomorphic. The diversity in ovary position among the species of *Topobea* considered here is suggestive of homoplasy and leads to some intriguing questions about the forces driving this kind of character evolution.

Another character of taxonomic importance in *Topobea* is the presence of foliar domatia. Nine of the twenty-nine Mesoamerican species of *Topobea* produce specialized pit, pocket, or hair tuft chambers (acarodomatia) in the vein axils of some or all abaxial leaf surfaces. The mite-leaf domatium association is generally a mutually beneficial relationship (Walter and Proctor 1999). The domatia provide shelter and protection for eggs and moulting mites. The mites evidently benefit the plants by feeding on fungal spores and the eggs of predaceous insects.

In addition to ovary position and meristic differences in petal, stamen, and ovary locules, a number of other characters are important for the delimitation and identification of *Topobea* species. These include size, shape, and degree of fusion of floral bracts, presence or absence of lateral anther sac fusion, modifications of the anther connective into appendages, and details of the anther pores. Staminal material is essential for generic placement and for definitive identification of many species. It has been necessary to use these characters in the key that follows despite the fact that all of them are not always available on every specimen. Because of this I have also tried, where possible, to include vegetative characters which are more readily accessible.

Information on the reproductive biology of *Topobea* is available for only two species, *T. brenesii* and *T. maurofernandeziana* (including *T. durandiana* as reported in Lumer 2000). Both of these species are endemic to Mexico and/or Central America. According to Lumer (2000), these two species are self-compatible and capable of producing viable seeds without outcrossing. Lumer found that experimentally selfed flowers of *T. brenesii* produced significantly more seeds than outcrossed flowers. The showy flowers of both species offer pollen as the primary reward which attracts several species of bees despite interspecific flower differences in size and texture. The bee pollinators of *Topobea* use the same buzzing method of pollen collecting that is widespread among the melastomes and other flowering plants with poricidal anthers. Bees alight on the flowers, bend their bodies over the anther cluster, and vibrate their indirect flight muscles in a way that results in rapid evacuation of pollen from the terminal anther pores of a flower. The ejected pollen is deposited on the bee's ventral side and readily transferred to the stigma of the next flower visited (Lumer 2000). Because both species of *Topobea* studied are self-compatible, insect-mediated selfing may constitute a significant factor in effecting optimal pollination and seed set.

KEY TO THE OCTANDROUS AND DODECANDROUS SPECIES OF *TOPOBEA*

- 1. Flowers 4-merous and diplostemonous (with eight stamens per flower); ovary 4-locular *T. tetramera*
- 1'. Flowers 6-merous and diplostemonous (with twelve stamens per flower); ovary 4-locular or 6-locular.
 - 2. Outer floral bracts conspicuously decurrent on and imparting a winged aspect to the floral peduncle *T. mcphersonii*
 - 2'. Outer floral bracts not conspicuously decurrent on the floral peduncle.
 - 3. Both surfaces of mature leaf blades moderately to copiously covered with smooth ferruginous hairs 0.5–3(–9) mm long.
 - 4. Mature leaves of a pair markedly unequal in size with the larger blade commonly six to twelve times the size of the smaller blade; floral peduncle 0.8–1.4 cm long; inner floral bracts fused basally for 3.5–5 mm to form a bowl-like collar; petals 0.5–0.6 0.5 cm; anthers 1.5–3 mm long *T. dimorphophylla*

- 4'. Mature leaves of a pair somewhat unequal in size with the larger blade typically not more than two or three times the size of the smaller blade; floral peduncle 3.5–5.2 cm long; inner floral bracts free to the base; petals 1.6–2.3 1.4–1.7 cm; anthers 5–7.5 mm long *T. intricata*
- 3'. Both surfaces of mature leaf blades not covered with ferruginous smooth hairs.
5. Some or all mature leaf blades typically bearing domatia (pit, pocket, or hair tuft domatia) on the abaxial surface in the basal angles between the median vein and each of the two proximal lateral veins.
6. Anther sacs laterally connate for half or more of their length.
7. Mature leaf blades bearing hair tuft domatia on the abaxial surface in the angles between the median vein and each of the two proximal veins; each anther with two confluent apical pores; connective dorso-basally appendaged; ovary 6-locular.
8. Uppermost cauline nodes covered with caudate-acuminate stipuliform flaps ca. 3 mm long that envelop caducous tufts of hairs, the distal portions of each flap \pm caducous with age and leaving a prominent interpetiolar ridge or corky line; outer floral bracts fused at the base for 4–6 mm; anthers 6–9 mm long. *T. multiflora*
- 8'. Uppermost cauline nodes not as above; outer floral bracts free from one another; anthers 4–5 mm long *T. pluvialis*
- 7'. Mature leaf blades bearing perforated pit domatia on the abaxial surface in the angles between the median vein and each of the two proximal lateral veins; each anther with two separate apical pores; anther connective simple and unappendaged; ovary 4-locular *T. parvifolia*
- 6'. Anther sacs completely free from one another.
9. Some or all abaxial foliar surfaces bearing hair tuft domatia that are sparsely to moderately covered with barbellate hairs in the angles formed between the median vein and the proximal pair of lateral veins.
10. Anthers 2.5 mm long, the surface granulose along the lower ventral half of the thecae; each anther with a solitary apical pore; connective prolonged dorso-basally into a deflexed caudiform appendage; ovary 6-locular. *T. lentii*
- 10'. Anthers 5–7 mm long, the surface smooth throughout the length of the thecae; each anther with two confluent apical pores; connective simple and unappendaged; ovary 4-locular *T. calycularis*
- 9'. Some or all abaxial foliar surfaces bearing pit or pocket domatia that lack hairs of any kind.
11. Calyx consisting of a truncate flange or broadly flattened into low undulations; each anther terminating in two confluent pores. *T. laevigata*
- 11'. Calyx consisting of well-defined lobes; each anther terminating in a solitary pore. Principal leaves markedly dimorphic in size at each node, the larger blades broadly rounded and \pm subpeltate at the base *T. dodsonorum*
- 12'. Principal leaves not markedly dimorphic in size at each node, all mature blades acute to obtuse at the base.
13. Outer floral bracts 4.5–7.5 \times 3–4 mm; petals 12–15 mm long; anther connective unappendaged; ovary 6-locular *T. suaveolens*
- 13'. Outer floral bracts 1.2–2.5 \times 1.5–2.5 mm; petals 7–8.5 mm long; anther connective prolonged dorso-basally into a \pm horizontal toothlike appendage 0.5 mm long; ovary 4-locular *T. pittieri*
- 5'. Mature leaf blades lacking domatia on the abaxial surface in the basal angles between the median vein and each of the two proximal lateral veins.
14. Calyx lobes 13–17 mm long, covered with a dense indument of spreading barbellate or plumose hairs.
15. Mature leaf blades dentate at least distally; anthers laterally connate for much of their length, each anther sac with 2 confluent, dorsally-inclined pores; ovary apex modified into a glandular-puberulent fluted cone and collar 7–9 mm long *T. calophylla*
- 15'. Mature leaf blades entire; anthers free from one another, each anther with 2 divergent, dorsally-inclined apical pores; ovary apex glabrous and not elevated into a cone and stylar collar *T. aeruginosa*
- 14'. Calyx truncate and flangelike or with triangular or depressed-triangular lobes 1–5 mm long, glabrous or if pubescent then the indument not as above.
16. Floral bracts and calyx lobes strongly undulate-recurved apically; inner floral bracts fused basally for 7–8 mm; each anther with 2 divergent, dorsally-inclined apical pores *T. brenesii*
- 16'. Floral bracts and calyx lobes not strongly undulate-recurved apically; inner floral bracts free; each anther sac with 2 confluent, dorsally-inclined apical pores (if anther pores are divergent then the anther connectives are unappendaged).
17. Blades of the principal leaves broadly rounded to rounded-emarginate at the apex; abaxial foliar surfaces consistently but inconspicuously glandular-punctate *T. albertiae*
- 17'. Blades of the principal leaves typically acuminate but sometimes varying to acute or caudate at the apex; abaxial foliar surfaces not glandular-punctate.

- 18. Anthers of a flower all free from one another.
- 19. Anthers releasing pollen by a solitary apical pore.
 - 20. All mature leaf blades glabrous throughout, the transverse secondary veins on the abaxial surface spaced mostly 0.25 mm apart at the widest portion of the blade; ovary 4-locular. *T. fragrantissima*
 - 20'. Some mature leaf blades sparingly covered with a caducous indument of rusty brown subulate and conic hairs on the abaxial surface, the transverse secondary veins on the abaxial surface spaced 1-3 mm apart at the widest portion of the blade; ovary 6-locular *T. gerardoana*
- 19'. Each anther releasing pollen by two confluent apical pores.
 - 21. Calyx consisting of well-defined lobes.
 - 22. Mature leaf blades 21-25.3 × 11-14 cm; floral bracts glabrous, anther connective prolonged dorso-basally into a deflexed appendage; ovary apex elaborated into a sleeve-like distally lobulate collar 2-3 mm long *T. amplifolia*
 - 22'. Mature leaf blades 9.5-15 × 5-10 cm; floral bracts moderately to sparsely covered with an indument of caducous matted hairs; anther connective unappendaged; ovary apex lacking a collar. *T. standleyi*
 - 21'. Calyx consisting of a truncate flange or the lobes broadly flattened into low undulations *T. laevigata*
- 18'. Anthers of a flower laterally connate for half or more of their length.
 - 23. Anthers conspicuously granulose along at least the lower ventral half of the thecae; transverse secondary veins on the abaxial surface of mature leaf blades spaced 0.25-0.5 mm apart at the widest portion of the blade *T. watsonii*
 - 23'. Anthers smooth throughout; transverse secondary veins on the abaxial surface of mature leaf blades spaced 1-4 mm apart at the widest portion of the blade.
 - 24. Calyx tube (fused portion of calyx below the free lobes) 6-8 mm long; filaments 7-9 mm long; anther thecae linear-oblong; ovary apex covered with a caducous ring of minute glandular hairs surrounding the stylar scar *T. maurofernandeziana*
 - 24'. Calyx tube 2-4 mm long; filaments 9-12 mm long; anther thecae subulate; ovary apex elevated into a cone about 2 mm long and a shallow collar about 0.5-0.75 mm long that may disappear as the ovary enlarges on mature fruits. *T. parasitica*

1. *Topobea aeruginosa* (Standl.) L. O. Williams, Fieldiana Bot. 31:35. 1965.

Blakea aeruginosa Standl., Field Mus. Nat. Hist., Bot. Ser. 17:381. 1938.

TYPE. — HONDURAS. Comayagua: near the summit of the ridge above El Achote, 1850 m, 1 Aug. 1936, *Yuncker et al.* 6267 (holotype: F!; isotypes: K!, NY!, US!).

Tree (or epiphytic shrub, fide Yuncker) 3-10 m tall. Upper cauline internodes bluntly quadrate. Uppermost internodes, vegetative buds, petioles, peduncles, and floral bracts densely covered with a ferruginous indument of barbed or plumose hairs. Leaves coriaceous when dry, 10-23.5 × 4.5-17 cm, elliptic-oblong to elliptic-ovate, the apex short-acuminate, the base obtuse to rounded, the margin entire, 5-7-nerved, the outermost pair of primaries often concealed by revolute foliar margins when dry, the blade adaxially glabrous and glossy, abaxially covered with barbed or plumose hairs. Flowers solitary or paired in axils of upper branchlets; peduncles 1.7-3 cm long. Outer floral bracts 1.5-2.6 × 1-1.5 cm, free or fused basally for 3-5 mm, lanceolate, the apex long-attenuate; inner bracts 1.5-1.8 × 1 cm, free, ovate, the apex long-acuminate. Calyx lobes linear-oblong, 1.3-1.5 cm long. Petals 6, glabrous but caducously ciliate, 1.5-1.7 × 0.5-0.8 cm, pink, obovate, the apex rounded. Stamens 12; filaments 0.7-0.8 cm long; anthers free, 0.9-1.1 cm long, 1 mm wide, yellow, linear-oblong, each with 2 divergent, dorsally-inclined apical pores; connective elevated dorso-basally into a blunt oblong appendage 0.5-1 mm long. Ovary completely inferior, 6-locular, glabrous and not elevated into a cone or stylar collar. Style glabrous, 1.5-1.8 cm long; stigma punctiform. Mature berry 1.3-1.5 × 1-1.3 cm. Seeds 1 mm long, brown, cuncate to narrowly pyriform.

DISTRIBUTION AND PHENOLOGY. — Local in cloud forests of Honduras and Nicaragua at 1200-1500 m. Flowering and young fruiting specimens have been collected from July through December.

REPRESENTATIVE SPECIMENS EXAMINED. — NICARAGUA. Matagalpa: camino a Aranjuez a menos de 1 km de carretera Matagalpa-Jinotega, 13°02'N, 85°55'W, 2 Jul. 1980, *Moreno 1028* (CAS); along road to La Fundadora, Cordillera Central, 22 Feb. 1963, *Williams et al. 24886* (F).

DISCUSSION. — This species is apparently known only from the type in Honduras. It is readily recognized by its rusty brown indument of plumose hairs on vegetative buds, abaxial leaf surfaces, floral peduncles, floral bracts and calyx lobes. Its free anthers are also distinctive in having two divergent apical pores.

2. *Topobea albertiae* Wurdack, *Phytologia* 55:146. 1984.

TYPE. — COLOMBIA. Antioquia: Fincas Montepinar and Las Palmas, Vereda Quebrada Larga, municipio Guatapé at the line with municipio San Rafael, elev. 1800 m, 4 Sep. 1982, *Albert de Escobar et al. 2278* (holotype: HUA; isotype US!)

Epiphytic shrub 2.5–3 m tall or reportedly a tree 5–12 m tall. Uppermost branchlets quadrate becoming rounded with age, the young vegetative buds and uppermost nodes covered with caducous simple hairs. Nodes on older branches becoming notably thickened with elevated interpetiolar lines or ridges. Mature leaves of a pair essentially equal or only somewhat unequal in size, glabrous adaxially but inconspicuously glandular-punctate abaxially; petioles 1–3.8 cm long; blades coriaceous, 5.7–16(–19) × 3.7–9.2(–12) cm, obovate to elliptic-obovate to elliptic, the apex rounded to rounded-emarginate, the base broadly acute to obtuse, the margin entire and sometimes revolute when dry, 5-nerved, the transverse secondary veins spaced 1–2.5 mm apart at the widest portion of the blade. Flowers erect, borne in clusters of 2–4 in each leaf axil of uppermost branches; peduncles 1.1–1.5 cm long, commonly lenticellate distally. Floral bracts erect, concave and closely enveloping the hypanthium, essentially glabrous or sparsely and caducously covered with a mixture of appressed hairs 0.5–1 mm long and amorphous branlike hairs, the margin often fimbriate-ciliolate; outer bracts 8–10 × 10 mm, fused basally for 3–5 mm, ± oblong to oblate, with a mostly rounded-truncate apex that sometimes varies to bluntly acute; inner bracts 7–10 × 10 mm, free but imbricate, ovate to oblate, the apex ± truncate to broadly rounded. Hypanthium (at anthesis) cupulate, 4–5 × 5 mm. Calyx tube 5–6 mm long, erect and ± cylindrical; calyx truncate and without evident lobes. Petals 6, glabrous and reflexed, 1.8–2.8 × 1.4–1.9 cm, pale pink or white flushed with pink, the claw typically white, obovate, the apex ± truncate-rounded, the margin caducously ciliolate. Stamens 12, the filaments 1.4–1.7 cm long, declinate, complanate, glabrous; anthers laterally connate for about half their length and forming a subparallel horizontal platform, 10–13 × 0.75–1 mm, yellow, oblong-subulate, each with 2 confluent, dorsally-inclined apical pores; connective thickened dorsally and prolonged dorso-basally into an acute appendage 2–2.5 mm long. Ovary superior or 1/2- to 1/3-inferior, (3–)4(–5)-locular, elevated into a cone 4–5 mm high but lacking a collar. Style glabrous 1.7–2 cm long, stigma punctiform. Mature berries and seeds not seen.

DISTRIBUTION AND PHENOLOGY. — Local in cloud forests of central Panama to Colombia at 100–2300 m. Collected in flower in January, February, July, and from October through December, in fruit from January through April and October through November.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Coclé: area of El Valle, 2 km E of La Mesa, N slope of Cerro Gaital, 8°38'N, 80°7'W, 16 Nov. 1983, *Churchill 3870* (CAS). Darién: Serranía del Darién, just below Cerro Mali, *Gentry et al. 16841* (DUKE). Panamá: near Cerro Jefe about 0.5–2 miles beyond road junction on the dirt road to Alto Pacora, 9°15'N, 79°30'W, 11 Jan. 1989, *Almeda et al. 6153* (CAS, PMA).

DISCUSSION. — This species is distinctive in having glandular-punctate abaxial leaf surfaces, a cylindrical calyx tube that lacks well-defined calyx lobes, and anther thecae that are laterally connate for a portion of their length. The flowers are also extraordinary in producing a clove-like fragrance remi-

niscent of that encountered in some neotropical orchids that attract euglossine bees. *Topobea albertiae* is unusually variable in characters which are typically constant and diagnostic among its congeners. For example, the number of ovary locules in most specimens examined is four but some flowers have only three locules and others have as many as five. The degree of ovary fusion to the hypanthial wall is equally puzzling because the ovary is completely superior in some flowers examined and 1/2 to 1/3 inferior in other flowers.

3. *Topobea amplifolia* Almeda, sp. nov. (Fig. 1)

TYPE. — COSTA RICA. Limón: Cantón de Talamanca. Bratsi, Amubri, Alto Lari, Kivut. Afluente innominado del Río Lari, margen izquierda, 9°23'25"N, 83°04'25"W, 1200 m, 21 Mar. 1992, *Herrera 5407* (holotype, CAS!; isotypes, CR, INB!, MO!).

Arbor 6 m alta. Petioli 3–5 cm longi, lamina 21–25.3 × 11–14 cm elliptica vel elliptico-ovata apice acuminata vel acuta basi acuta vel obtusa, 5–7-nervata ad maturitatem chartacea et glabra, nervis secundariis 0.25 mm inter se distantibus. Flores 6-meri in quoque nodo superiore 4–5, pedunculis 1.3–2 cm longis, bractee exteriores 0.8–1.2 × 0.7–0.9 cm ovatae vel elliptico-lanceolatae ca. 3 mm coalitae apice truncato-rotundata plerumque acuto vel cuspidato; bractee interiores 0.9 × 1 cm omnino liberae. Hypanthium (ad torum) 0.8–0.9 longum; calycis tubus 2–3 mm longum, lobis 3–4 mm longis. Petala alba, 1.9 × 1.3 cm oblongo-ovata vel obovata. Filamenta 6 mm longa; antherae 6 × 2 mm inter se non cohaerentes, dorsaliter biporosae; connectivum ad basim dorsaliter 1 mm descendenti armatum. Stylus 1.5 cm; ovarium 6-loculare et 2/3 inferum, collo 2–3 mm alto glabro.

Reportedly a tree 6 m tall. Uppermost branchlets with thickened interpetiolar ridges at each node, the internodes rounded-quadrate becoming rounded with age. Vegetative and very young floral buds copiously but caducously covered with an amorphous rusty brown scurfy indument. Mature leaves of a pair essentially equal or only slightly unequal in size, glabrous throughout; petioles 3–5 cm long; blades chartaceous, 21–25.3 × 11–14 cm, elliptic-ovate to elliptic, the apex acuminate to abruptly acute, the base acute to obtuse, the margin inconspicuously crenulate, 5–7-nerved, the outermost intramarginal pair commonly depressed and inconspicuous; the transverse secondary veins spaced 0.25 mm apart at the widest portion of the blade. Flowers erect to spreading, borne in clusters of four or five in each leaf axil of distal branches; peduncles 1.3–2 cm long. Floral bracts glabrous, closely enveloping the hypanthium; outer bracts 0.8–1.2 × 0.7–0.9 cm, fused basally for 3 mm, ovate varying to elliptic-lanceolate, the apex abruptly acute to cuspidate; inner bracts 0.9 × 1 cm, free, depressed-ovate to suborbicular, the apex commonly retuse and often mucronate. Hypanthium (at anthesis) campanulate, 0.8–0.9 × 0.8–0.9 cm. Calyx tube 2–3 mm long; calyx lobes (fruiting hypanthium), erect, 3–4 mm long and 3–4 mm wide basally, oblong-ovate, rounded apically and covered with callose-thickened teeth at the abaxial apex. Petals 6, glabrous, 1.9 × 1.3 cm, white, obovate, the apex rounded, entire. Stamens 12; filaments complanate and glabrous, 6 mm long; anthers free, 6 × 2 mm, reportedly yellow-brown, subulate, each with 2 confluent, dorsally-inclined apical pores; connective thickened dorsally and prolonged dorso-basally into a deflexed tooth-like appendage 1 × 0.25 mm. Ovary 2/3 inferior, 6-locular, elaborated apically into a glabrous, sleeve-like distally lobulate collar 2–3 mm long. Style glabrous, 1.5 cm long; stigma ± clavate and obliquely flattened when dry. Immature berry 0.8 × 1 cm. Seeds cuneate to narrowly obovoid, 1 mm long, brownish with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Known only from low-elevation rainforest in southeastern Costa Rica near the Panamanian border at 1200 m. The type and only known collection, which was made in March, is in flower and young fruit.

DISCUSSION. — The distinctive features of *T. amplifolia* include the closely spaced (0.25 mm) transverse secondary veins on abaxial foliar surfaces (Fig. 1B), callose-thickened teeth at the abaxial

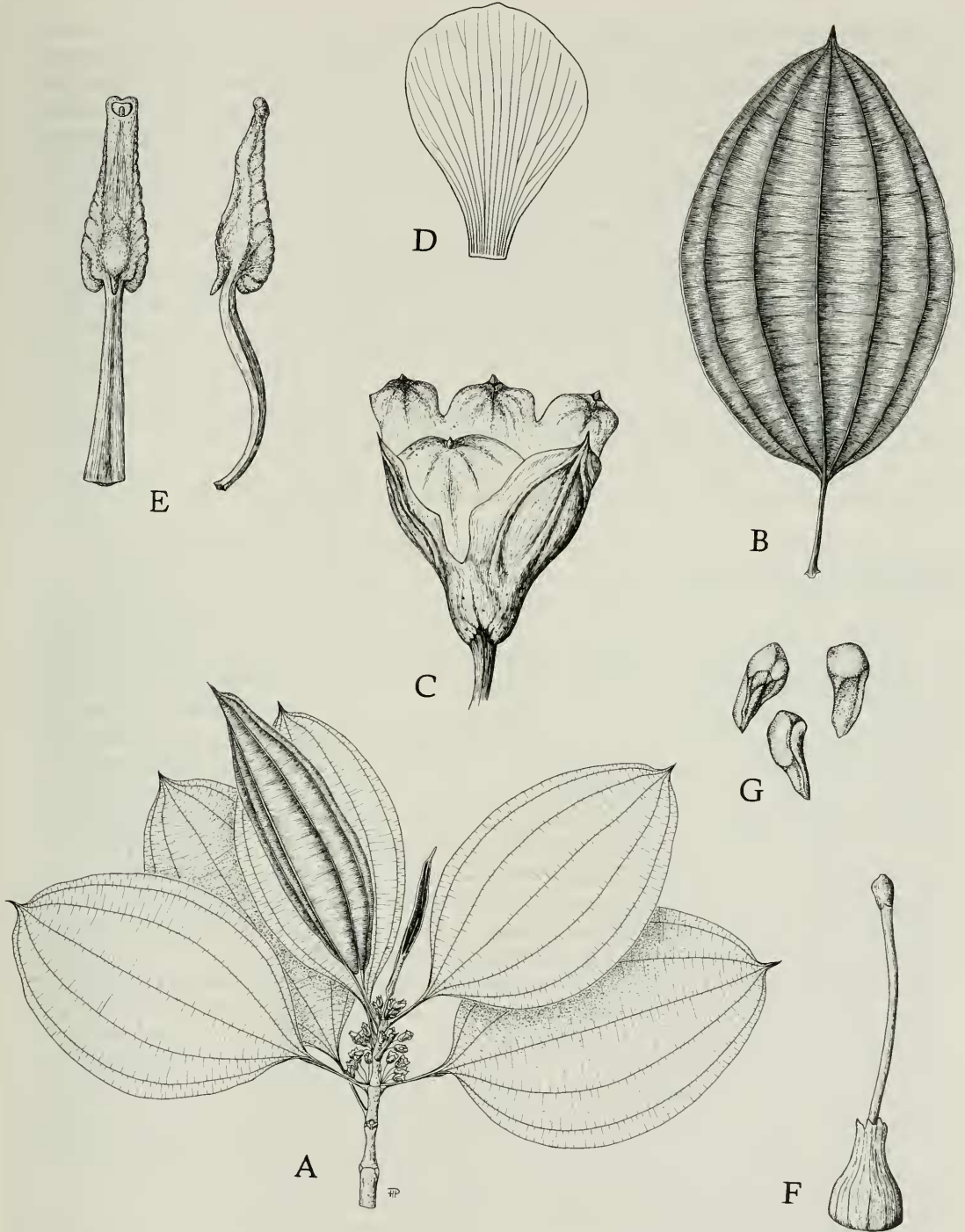


FIGURE 1. *Topobea amplifolia* Almeda. A. habit, ca. 1/5; B. representative leaf (abaxial surface, ca. 1/3; C. young fruiting hypanthium with decussate floral bracts, ca. 3; D. petals (adaxial surface), 2; E. stamens, dorsal view (left) and profile view (right), 5; F. stylar collar, style, and stigma, 3; G. seeds, 15. (A–G from Herrera 5407.)

apex of each calyx lobe (Fig. 1C), dorso-basally appendiculate anther connectives (Fig. 1E), and distally lobulate collar that envelops the style base (Fig. 1F). Among Mesoamerican species, it most resembles *T. multiflora* that differs in having hair tuft domatia on abaxial foliar surfaces, stipuliform nodal flaps, pink petals, and anther thecae that are laterally connate for at least half of their length. *Topobea amplifolia* is also superficially similar to *T. superba* Naudin of Colombia and *T. subscaberula* Triana of Colombia and Ecuador. The former differs by its nodal stipuliform flaps (1–2 mm long), hair tuft acarodomatia with roughened hairs 1–2.5 mm long where primary leaf veins diverge from one another abaxially, secondary transverse veins spaced 1.5–4 mm apart, and anther thecae that are laterally coherent for about half of their length. *Topobea subscaberula* differs from *T. amplifolia* in having young leaves and pedicels that are moderately but caducously puberulous with pinoid hairs 0.1–0.2 mm long, primary leaf vein divergence (abaxial) covered with roughened hairs about 1 mm long, secondary transverse veins spaced 2–2.5 mm apart, apically obtuse outer floral bracts, and an ovary apex that is elevated into a broad crateriform dome but not elaborated into a lobulate collar.

ETYMOLOGY. — The epithet *amplifolia* is derived from the Latin words *amplus*, ample or large, and *folius*, -leaved, in reference to the large leaves of this species.

4. *Topobea brenesii* Standl., Field Mus. Nat. Hist., Bot. Ser. 18:842. 1938.

TYPE. — COSTA RICA. Alajuela: La Palma de San Ramón, 1250 m, 13 Mar. 1929, *Brenes 6732* (holotype: F!; isotypes: CR!, NY!).

Epiphytic shrub 2–4 m tall. Uppermost branchlets rounded-quadrate becoming rounded with age, the uppermost internodes, young vegetative buds, pedicels, floral peduncles, floral bracts (especially abaxial surfaces), hypanthia, and calyx lobes copiously covered with a caducous mixture of elongate roughened hairs and less conspicuous stellulate or branlike hairs, the upper cauline nodes copiously setose with mostly smooth or sparingly roughened hairs. Mature leaves of a pair equal to somewhat unequal in size; petioles 0.2–0.7 cm long; blades coriaceous, 4.5–14 × 2.1–6.7 cm, obovate to elliptic, the apex rounded to obtuse or acute, the base broadly rounded to truncate, margin entire, blade 3-nerved or if 3-plinerved then the inner pair of primary veins diverging from the median vein 0.6–1 cm above the blade base (on abaxial surface), the transverse secondary veins spaced 1.5–3 mm apart at the widest portion of the blade, the blade adaxially covered with a sparse cover of elongate roughened and branlike hairs but commonly glabrous at maturity, abaxially sparsely covered with elongate roughened and branlike hairs especially on the elevated primary veins. Flowers erect, 1 to 3 in each leaf axil of distal branches; peduncles 0.2–1.3 cm long. Floral bracts closely enveloping hypanthium and strongly undulate-recurved apically; outer bracts 8–9 × 6.5–7 mm, free or fused basally for 0.5–1 mm, broadly oblong; inner bracts 9–10 × 13–14 mm, fused basally for 7–8 mm, semi-circular. Hypanthium (at anthesis) campanulate, 7–8 × 7–8 mm. Calyx tube 3–4 mm long, erect and cupulate to campanulate; calyx lobes 4 × 4–6 mm, oblong and rounded at the recurved apex. Petals 6, glabrous, 1–1.5 × 0.5–1.4 cm, pale pink, obovate. Stamens 12; filaments 4–6 mm long, declinate and glabrous; anthers free, 4.5–5.5 × 1 mm, yellow, each opening by 2 divergent, dorsally-inclined pores; connective thickened dorsally and prolonged dorso-basally into a horizontally divergent or recurved knobby appendage 0.5 mm long. Ovary wholly superior, 6-locular, elevated at the glabrous apex into a lobulate rimlike collar that forms a wide circle around the stylar scar. Style glabrous, 1.2–1.4 cm long; stigma punctiform. Berry 1–1.2 × 1–1.2 cm. Seeds narrowly ovoid to cuneate, 1–1.25 mm long, beige with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Endemic to Costa Rica where it is local and uncommon in cloud forests of the Cordillera de Tilarán and adjacent slopes southeast to the San Ramón region and east to the western slopes of Volcán Viejo in the Cordillera Central at 950–1560 m. Collected in

flower from January through April, in fruit from January through April, July, August and probably intervening months.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela: Cantón de San Ramón. Los Angeles, Colonia Palmareña. Cuenca media de Río San Lorenzo, camino a la mina de yesa, 10° 12' 50" N, 84° 35' 15" W, 20 Feb. 1991, *Herrera et al.* 4918 (CAS, CR, INB, MO); Cantón de San Carlos, Zapote, 31 Oct. 1938, *A. Smith 1306* (CAS, NY). Puntarenas: Cordillera de Tilarán. Selectively logged pasture known locally as the Bull Pen about 0.5–1 km downslope from Monteverde Cloud Forest Reserve Station, 29 Feb. 1992, *Almeda & Daniel 7185* (CAS, CR).

DISCUSSION. — This species is known only from the Cordillera de Tilarán south and east to the San Ramon and Volcán Viejo regions of Costa Rica. It is easily recognized by its completely superior ovary, leaf blades that are rounded to truncate basally, conspicuously appendiculate anther connectives, and undulate-recurved floral bracts and calyx lobes.

5. *Topobea calophylla* Almeda, Proc. Calif. Acad. Sci. 43:281. 1984.

TYPE. — PANAMA. Veraguas: 5 mi. W of Santa Fé on road past Escuela Agrícola Alto Piedra on Pacific side of divide, elev. 800–1200 m, 18 Mar. 1973, *Croat 23000* (holotype: CAS!; isotype: MEXU!, MO!, US!).

Coarse epiphytic shrub. Upper branches rounded to subquadrate. Distal internodes, vegetative buds, peduncles, and floral bracts covered with a hirsute indument of ferruginous barbellate hairs mostly 3–9 mm long. Mature leaves of a pair somewhat unequal in size; blades firmly chartaceous to coriaceous, 14.5–37.5 × 8.6–17.8 cm, elliptic-ovate, 5–7-nerved, the elevated transverse secondary veins spaced 4–7 mm apart at the widest portion of the blade, adaxially glabrous, abaxially moderately hirsute with barbellate hairs mostly 1–3 mm long, the apex abruptly caudate-acuminate, the base rounded to subcordate, the margin inconspicuously dentate. Flowers erect to widely spreading, paired or borne in clusters of three to four in leafy axils of distal branches; peduncles 2.8–4 cm long. Floral bracts foliaceous, entire, 2–5-nerved, free, each pair closely subtending one another or separated on the peduncle by a distance of 3–4 mm. Outer bracts 1.7–2.3 × 1.5–1.7 cm, elliptic-ovate, the apex acuminate; inner bracts 1.6–1.9 × 1.3–1.7 cm, elliptic-ovate, the apex acute to acuminate. Calyx lobes lance-triangular, 14–17 × 5–6 mm. Petals 6, glabrous, entire but sparingly glandular-ciliate, 2 × 1 cm, reportedly pink, ± spatulate, the apex acute to obtuse. Stamens 12, filaments 5 × 1.5 mm, strongly declinate; anthers laterally connate for a good portion of their length, 8 × 1.5 mm, yellow (?), linear-subulate, each with 2 confluent, dorsally-inclined apical pores; connective thickened dorsally near the filament insertion into a blunt callosity. Ovary completely inferior, 6-locular, apex prolonged into a glandular-puberulent fluted cone and stylar collar mostly 7–9 mm long. Style glabrous, 11–14 × 1 mm; stigma capitate to truncate, the actual surface appearing somewhat crateriform. Mature berry not seen.

DISTRIBUTION AND PHENOLOGY. — Locally common in rainforests and cloud forests from the vicinity of Fortuna Dam to the Santa Fé region of Veraguas disjunct to Comarca de San Blas in north-central Panama at 10–1200 m. Collected in flower from February through August, in fruit during March and July.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Bocas del Toro: vicinity of Fortuna Dam, below pass on Chiriquí Grande road, 8° 45' N, 82° 15' W, 27 June 1986, *McPherson 9714* (CAS, MO, PMA). Comarca de San Blas: Cerro Brewster, 9° 18' N, 79° 16' W, 21 Apr. 1985, *de Nevers et al.* 5384 (CAS, MO); Río Taindi (Taimdi of maps), 6 km above confluence with Río Mandinga, 9° 25' N, 79° 11' W, 5 Apr. 1986, *de Nevers & Herrera 7638* (CAS, MO, PMA). Veraguas: Distrito de Santa Fé, alrededores del Río Primer brazo de Ulaba, 8° 33' N, 81° 07' W, 6 Jul. 1996, *Galdames et al.* 3145

(CAS, SCZ): Boca de Concepción, in Golfo de los Mosquitos, forest near river, 8°50'N, 81°00'W, 6 Aug. 1987, *McPherson 11394* (CAS, MO, PMA).

DISCUSSION. — This large-leaved Panamanian endemic has an unusual indument of long, spreading, barbellate hairs on distal internodes, young buds, peduncles, and floral bracts. This together with the laterally connate anther thecae, and glandular-puberulent fluted ovary cone and stylar collar at the ovary apex make it a standout among Mesoamerican species. For an illustration of this species see Almeda (1984:280).

6. *Topobea calycularis* Naudin, Ann. Sci. Nat. Bot. 3, 18:149. 1852.

TYPE. — MEXICO. Chiapas: Zuluzuchiapas, *Linden 650* (holotype: P!, fragment at BR!; isotype: K!).

Epiphytic shrub or tree 2–13 m tall. Uppermost branchlets quadrate and carinate on the angles becoming rounded with age, essentially glabrous throughout, the young floral bract margins, floral buds, and calyx rim sometimes covered with a caducous furfuraceous indument of stellulate or matted fimbriate branlike hairs. Mature leaves at a node somewhat unequal in size (the larger sometimes twice the size of the opposing one); petioles 1.3–4 cm long; blades coriaceous, 4.5–17.2 × 2.1–10 cm, elliptic to elliptic-obovate, the apex abruptly acuminate, the base acute, the margin entire, 3–5-plinerved with the innermost primaries diverging from the median vein 0.4–1.5 cm above the blade base (on abaxial surface) with hair tuft acarodomatia that are sparsely to moderately covered with robust shaggy hairs (0.25–0.5 mm long) in the angles formed with the median vein, the transverse secondary veins spaced 0.5–1 mm apart at the widest portion of the blade. Flowers erect, solitary or in clusters of 2 to 4 in each leaf axil of distal branches; peduncles 4–9 mm long. Floral bracts ± concave and closely enveloping the hypanthium; outer bracts 3–5 × 4–5 mm, fused basally for 1.5–2 mm, rounded-triangular to ovate; inner bracts 3.5–4 × 4–5 mm, free but partly imbricate, semi-circular. Hypanthium (at anthesis) campanulate, 4.5 × 4.5 mm. Calyx tube 2–3 mm long, erect and cupulate, calyx broadly flattened into low apiculate undulations 0.5 × 2 mm. Petals 6, glabrous, 1–1.3 0.3–0.6 cm, white, narrowly obovate, the margin fimbriate. Stamens 12; filaments 6–7 mm long, declinate and glabrous; anthers free, 5–7 × 0.75 mm, yellow, each with 2 confluent, dorsally-inclined pores at the apex; connective thickened dorsally, unappendaged or with a minute dorso-basal callosity. Ovary 1/3 inferior, 4-locular, apex glabrous, stylar scar evident but not elevated into a prominent cone or stylar collar. Style glabrous, 1–1.5 cm long; stigma punctiform. Berry 0.9–1.1 × 0.8–1 cm. Seeds narrowly pyriform to narrowly ovoid, 1 mm long, beige with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Often common in lowland and montane rainforests from Chiapas, Mexico east to Guatemala (Izabal) at 320–1625 m. Collected in flower from January through May and in November and December, in fruit from February through August, December and probably most intervening months.

REPRESENTATIVE SPECIMENS EXAMINED. — GUATEMALA. Alta Verapaz: Chapultepec Farm, 62 km beyond Cobán on Sebol road, 20 May 1964, *Contreras 4730* (CAS, LL); Pansamála, Feb. 1887, *von Tuerckheim 1135* (DS, NY, US). Izabal: Municipio El Estor La Cumbre, al NE del Estor, 17 Jul. 1988, *Tenorio et. al. 14516* (CAS, MEXU). MEXICO. Chiapas: Municipio La Trinitaria, Lagos de Montebello National Park, 19 Nov. 1980, *Breedlove & Almeda 47572* (CAS, MEXU); Municipio of Ocosingo 70 km SW of Palenque on road to Ocosingo along the Jol Uk' um, *Breedlove & Almeda 48335* (CAS, MEXU); Municipio of Peltalcingo, slope of Ahk' ulbal Nab above Peltalcingo, *Breedlove 50462* (CAS, MEXU); Municipio of Independencia, 45–50 km E of Lagos de Montebello National Park on road to Ixcán from Santa Elena, *Breedlove & Almeda 57731* (CAS, MEXU); Municipio de Tila, pie del Cerro Acavaina, *Ton 7347* (CAS, MEXU); Municipio Margaritas, Col. Maravilla, Tenejapa, *Ton 9084* (CAS, MEXU).

DISCUSSION. — *Topobea calycularis* is distinguished by its hair tuft foliar domatia, calyx lobes that consist of low apiculate undulations, essentially unappendaged anther connectives, and its 4-locular ovary. Only one collection examined, *Tenorio et al. 14516*, CAS, lacks good development of hair tuft domatia. *Topobea laevigata* is the only other species with which *T. calycularis* might be confused. In *T. laevigata*, the domatia, when produced, are slitlike pit domatia at the abaxial margin of the leaf blade near the petiole-laminar junction, and the ovary is consistently 6-locular.

For Costa Rican specimens erroneously identified as *T. calycularis*, see the discussion under *T. multiflora*.

7. *Topobea dimorphophylla* Almeda, sp. nov. (Fig. 2)

TYPE. — COSTA RICA. Heredia: along Río Peje about 0.5 km SW of back end of Vargas property; approximately in the area where an imaginary line drawn between Magsasay (colonia penal) and Puerto Viejo de Sarapiquí would cross the Río Peje, 20 Feb. 1982, *Hammel 11217* (holotype: CAS!; isotypes: CR!, DUKE!, INB!, MO!, US!).

Frutex hemiepiphyticus. Ramuli sicut pedunculi folia inflorescentia hypanthiaque pilis 1.5–3(–9) mm longis induti. Folia in quoque pari dimorpha papyracea distanterque denticulata 3–5-plinervata. Folia maiora: lamina (5.5–)9–15.5 × 2–7.5 cm elliptica vel elliptico-ovata apice caudato-acuminata basi rotundata. Folia minora: lamina 0.9–1.7 × 0.6–1 cm ovata vel subcordata apice caudato-acuminata basi cordata. Flores 6-meri in quoque nodo superiori singuli, pedunculis 0.8–0.9(–1.4) cm longis; bractee exteriores omnino liberae 0.5–0.7 × 0.3–0.5 cm elliptico-ovata apice acuto; bractee interiores 0.5–0.6 × 0.4–0.5 cm ovatae apice acuta ca. 3.5–5 mm coalitae. Calycis tubus 0.5–0.75 mm longus, lobis 0.7–0.9 × 0.2–0.3 cm. Petala 5–6 × 5 mm obovata vel subrotundata. Antherarum thecae 1.5–3 × 0.5–0.75 mm inter se non cohaerentes, dorsaliter biporosae; connectivum dorsaliter supra thecarum basim tuberculatum. Ovarium 6-loculare et omnino inferum apice glabro (cono et collo non evoluto).

Secondary hemiepiphytic shrub with main stems growing vinelike up trunks of host trees and secondary branches either drooping or horizontally spreading to 1–3 m long. Uppermost branchlets mostly terete, the older branches covered with numerous short root-like protuberances (adventitious roots?). Cauline internodes, leaf blades (both surfaces), peduncles, floral bracts, hypanthia, and calyx lobes copiously hirsute with rusty brown hairs mostly 1.5–3(–9) mm long. Mature leaves of a pair markedly unequal in size; blades coarsely papery when dry, the larger one at each node (5.5–)9–15.5 × 2–7.5 cm, elliptic to elliptic-ovate, the apex caudate-acuminate, the base broadly rounded, the margin denticulate (sometimes remotely so), 3-plinerved with an additional ill-defined intramarginal pair, the innermost pair of primary veins diverging from the median vein 2–3 mm above the blade base, the ± transverse secondary veins spaced 2–5 mm apart at the widest portion of the blade on the abaxial surface; petiole 5–17 mm long; the smaller blade 0.9–1.7 × 0.6–1 cm, ovate to subcordate, apex short caudate-acuminate, base cordate, margin entire, 3-nerved, the transverse secondary veins not evident on the abaxial surface; petiole barely prolonged or up to 2 mm long. Flowers erect, solitary in each axil of uppermost leaves; peduncles 0.8–0.9(–1.4) cm long. Floral bracts green and entire; outer bracts 0.5–0.7 × 0.3–0.5 cm, free, elliptic-ovate, the apex acute; inner bracts fused basally for 3.5–5 mm to form a bowl-like collar, the free lobes broadly ovate to deltoid, 0.5–0.6 × 0.4–0.5 cm. Hypanthium at anthesis 4–5 mm long to the torus and 4–5 mm in diameter. Calyx tube 0.5–0.75 mm long, ± erect at anthesis. Calyx lobes (on young fruit) deltoid at base but abruptly tapered to narrow linear upright segments 0.7–0.9 cm long and 0.2–0.3 cm wide at the base between sinuses. Petals 6, glabrous, 5–6 mm, translucent white, thin and translucent when dry, broadly obovate to subrotund, the apex ± rounded, the base shortly clawed, entire. Stamens 12, free and isomorphic; filaments 1.5–3 mm long,

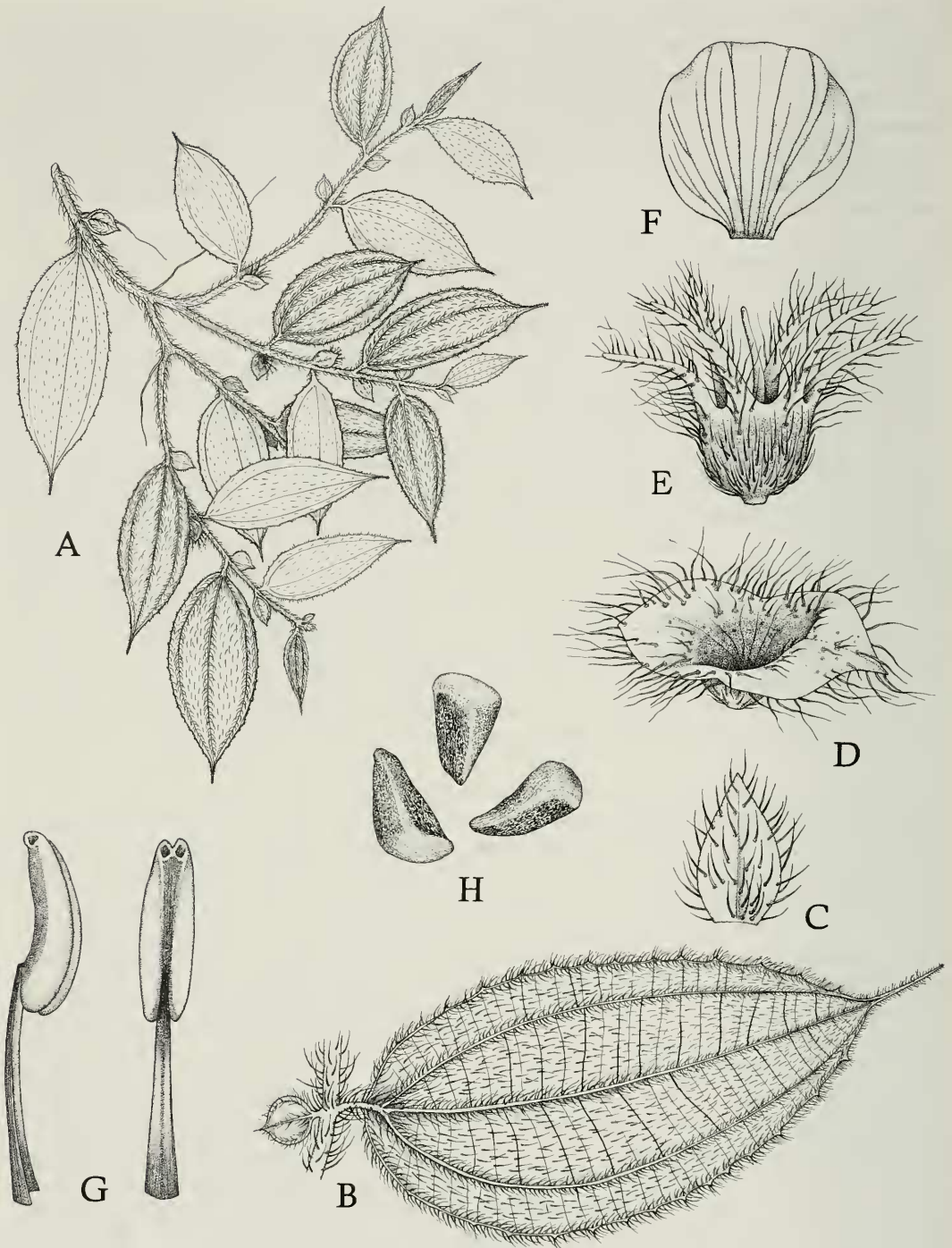


FIGURE 2. *Topobea dimorphophylla* Almeda. A. habit, 2/5; B. foliar dimorphism at a node, 2/3; C. outer floral bract, 5; D. inner floral bracts, 4; E. hypanthium (floral bracts removed), 3; F. petal (adaxial surface), ca. 5; G. stamens, profile view (left) and dorsal view (right) 12; H. seeds, 15. (A from Gomez *et al.* 21127; B from Grayum *et al.* 7932; C-G from Hammel 11217; H from Hammel & Trainer 13241.)

glabrous; anthers $1.5-3 \times 0.5-0.75$ mm, yellow, oblong, each with 2 confluent, dorsally-inclined pores at the apex; connective thickened dorsally and barely elevated into a blunt callose knob dorso-basally. Ovary completely inferior, 6-locular, glabrous at the apex which is barely elevated at the stylar scar. Style glabrous, declinate, 9–10 mm long; stigma punctiform. Berry red at maturity, $9-10 \times 9-10$ mm. Seeds 1 mm long, brown, cuneate to narrowly pyriform, testa smooth.

DISTRIBUTION AND PHENOLOGY. — Local and uncommon in the Caribbean slopes and lowlands of Costa Rica from the Puerto Viejo region south to the Cordillera de Talamanca (Limón) at 100–1000 m. Collected in flower and fruit from October through March and in June and July.

PARATYPES. — COSTA RICA. Alajuela: Reserva Biológica Monteverde Río Peñas Blancas, Laguna y Quebrada Celeste, $10^{\circ}20'N$, $84^{\circ}41'W$, 850 m, 4 Nov. 1989, *Bello 1459* (CAS); Reserva Forestal de Arenal, Quebrada San Gerardo, Río Caño Negro, $10^{\circ}23'N$, $84^{\circ}48'W$, 800 m, 18 Feb. 1990, *Bello 1909* (MO). Cartago: Valle Escondido, 720 m, 31 Mar. 1966, *Schnell 641* (CR, US). Heredia: Parque Nacional Braulio Carrillo, La Virgen, Sarapiquí, Sendero Transecto, $10^{\circ}16'N$, $84^{\circ}05'W$, 700 m, 11 Dec. 1988, *Ballester 53* (CAS, CR, INB). Parque Nacional Braulio Carrillo, Fila Carrillo – Sendero La Botella, 400–800 m, 15 Feb. 1984, *Gomez et al. 21127* (CAS, CR); Parque Nacional Braulio Carrillo, forest between Río Peje and Río Sardinalito on Atlantic slope of Volcán Barva, $10^{\circ}17.5'N$, $84^{\circ}05'W$, 700–800 m, 14 Nov. 1986, *Grayum & Herrera 7895* (CAS, CR); Finca La Selva, OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí 100 m, 18 Jul. 1982, *Hammel & Trainer 13241* (CAS, CR, DUKE). Limón: Cantón de Talamanca, Bratsi; Alto Lari, Entre Surayo y Dapari, 50 m N de la desembocadura del Río Dapari (Pare), junto al Río Lari, $9^{\circ}25'10''N$, $83^{\circ}03'00''W$, 300 m, 25 Feb. 1992, *Aguilar & Schmidt 961* (INB, MO); Suerre, Santa Clara, 300 m, Feb. 1896 (no exact day), *Donnell-Smith 6554* (F, US); Zona Protectora Barbilla on W side of plateau separating headwaters of N fork of Río Danta from headwaters of Quebrada Barreal, Río Barbilla drainage (SE of Siquirres), $10^{\circ}05'N$, $83^{\circ}28.5'W$, 600–660 m, 11 Jan. 1987, *Grayum et al. 7932* (CAS, CR, MO); Cantón de Talamanca, Bratsi, Amubri, Alto Lari, Kivut. Quebrada innominada, margen derecha del Río Dapari $9^{\circ}24'20''N$, $83^{\circ}05'35''W$, 1000 m, 11 Mar. 1992, *Herrera 5294* (CAS, CR, INB, MO).

DISCUSSION. — *Topobea dimorphophylla* has leaf blades that are markedly unequal in size at each node and copiously pubescent on both surfaces (Fig. 2A). It is most like *T. intricata* which has leaf blades that are only somewhat unequal in size at each node, longer floral peduncles (3.5–5.2 cm vs. 0.8–1.4 in *T. dimorphophylla*), and free (vs. basally fused for 3.5–5 mm) floral bracts. In habit, indument details, and the pronounced foliar dimorphism at each node, *T. dimorphophylla* is also similar to *T. tetramera* which is readily separated by its 4-merous flowers, 4-locular ovary, completely free inner and outer floral bracts, and truncate anther pores.

One collection of *T. dimorphophylla*, *Donnell-Smith 6554*, was erroneously cited as a representative specimen of *Clidemia costaricensis* Cogn. & Gleason ex Gleason (Gleason 1939:126). This appears to have been an inadvertent error because this specimen, which is not mixed with *C. costaricensis*, has young fruiting hypanthia with attached floral bracts that Gleason surely would have recognized as something other than *Clidemia*.

ETYMOLOGY. — The epithet *dimorphophylla* is derived from the Latin word *dimorphus*, having two forms, and the Greek word *phyllus*, relating to leaves, in reference to the pronounced difference in leaf size at each node.

8. *Topobea dodsonorum* Wurdack, *Phytologia* 38:304. 1978.

TYPE. — ECUADOR. Los Ríos/Pichincha border: near La Centinela at Km 12 on road from Patricia Pilar to Flor de Mayo, Montaña de Ila, 600 m, 16 Jul.–11 Aug. 1977, *Dodson & Dodson 6752* (holotype: US!; isotype: MO, SEL).

Viny epiphytic shrub often with pendent branches 1–1.5 m long. Uppermost branchlets terete with elevated interpetiolar ridges. Upper internodes, juvenile leaves, peduncles, bracts, and calyx lobes caducously scurfy-puberulent with branlike or stellulate hairs. Mature leaves of a pair markedly dimorphic in size; blades subcoriaceous, the larger at each node 7.4–19.5 × 3.6–9.5 cm, elliptic to ovate or subcordate, the apex acuminate, the base broadly rounded and subpeltate, the margin entire, 5–7-nerved with well-developed pocket domatia formed at the point where the innermost primaries diverge from the median vein, the transverse secondary veins spaced 1–2 mm apart at the widest portion of the blade on the abaxial surface; petiole 3–5 mm long; the smaller blade 1.4–5 × 0.8–2.8 cm, narrowly elliptic, the apex acuminate, the base rounded, the margin entire, 3–5-nerved with domatia like those of the larger leaves but smaller in all dimensions and less conspicuous, the transverse secondary veins not conspicuous on the abaxial surface; petioles 0.1–1.3 mm long. Flowers erect, solitary or borne in clusters of 2 to 3 in each leaf axil of distal branches; peduncles 1–2.5 cm long. Floral bracts fused basally for 0.5–1 mm and much shorter than the hypanthium and calyx; outer bracts 2–2.5 × 2 mm, ovate; inner bracts 2 × 2 mm, oblate to semicircular. Hypanthium (at anthesis) campanulate, 4 × 3–4 mm. Calyx tube 1–1.5 mm long; calyx lobes 1–1.8 × 2 mm, triangular. Petals 6, glabrous, 5–6 × 2–3.5 mm, yellow, yellow-brown or greenish brown, oblong-obovate to subspatulate with a blunt acute apex. Stamens 12; filaments 2–3.5 mm long, declinate and glabrous; anthers free, 1.75–2 × 0.5 mm, yellow, linear-oblong to somewhat subulate, each opening by a solitary, dorsally-inclined apical pore; connective thickened dorsally and prolonged dorso-basally into a blunt appendage 0.25 mm long. Ovary 1/2-inferior, 4-locular, somewhat elevated and rounded up to the stylar scar but lacking a cone and collar. Style glabrous, 7 mm long; stigma punctiform. Berry 5–7 × 6–7 mm, greenish flushed with maroon at maturity. Seeds cuneate to narrowly pyriform, 1 mm long, beige with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Often locally common in rainforests and low elevation cloud forests of western and north-central Panama and eastern Ecuador at 540–1200 m. Flowering collections have been made in January, February, April, June, July and September, fruiting during these same months and in November.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Chiriquí: Edwin Fabrega Dam and Reserve in Fortuna along trail to hydrological station along Rio Hornito, 8°45'N, 82°5'W, 20 Jan. 1989, *Almeda et al. 6351* (CAS, PMA). Comarca de San Blas: Cerro Brewster, 9°18'N, 79°16'W, 21 Apr. 1985, *de Nevers et al. 5459* (CAS, MO, PMA).

DISCUSSION. — The diagnostic features of *T. dodsonorum* include its pronounced foliar size dimorphism at each node, well-developed foliar pocket domatia, triangular calyx lobes, and 4-locular ovary. In his account of this species for Flora of Ecuador, Wurdack (1980) stated that domatia are lacking in the smaller leaf at each node. Although the domatia on the smaller leaf are smaller in all dimensions, I have found them to be present on all specimens examined from throughout the range of the species.

9. *Topobea fragrantissima* Almeda, *Proc. Calif. Acad. Sci.* 46:318. 1990.

TYPE. — PANAMA. Chiriquí: vicinity of Fortuna Dam, along trail across valley of Rio Hornito, elev. 1100–1250 m, 12 Mar. 1988, *Almeda et al. 6086* (holotype: CAS!; isotypes: CR!, F!, MO!, PMA!, TEX!, US!).

Epiphytic or terrestrial shrubs or small trees 1.5–4 m tall. Distal branchlets subquadrate and glabrous with interpetiolar ridges or lines. Vegetative buds and young leaves sparingly and caducously lepidote-furfuraceous. Mature leaves of a pair equal to somewhat unequal in size, glabrous throughout, 1.5–5.5 cm long and 1.6–3 cm wide, elliptic to elliptic-obovate, the apex acuminate, the base acute, the margin entire, 3-nerved or 3-plinerved abaxially with an additional submarginal pair of inconspicuous veins, secondary veins spaced mostly 0.25 mm apart at the widest portion of the blade. Flowers erect, solitary or paired in leaf axils of upper branches; peduncles 2–3 cm long, glabrous; outer bracts 5–11 × 3–5 mm, free, elliptic or rarely varying to obovate, glabrous, apex rounded; inner bracts 4–6 × 4–5 mm, free, obovate, glabrous, apex broadly rounded. Calyx tube 1 mm long; calyx lobes 1 mm long and 1–1.5 mm wide basally, ovate to deltoid-ovate with a blunt callose-thickened tooth on the abaxial apex of each lobe, margin entire but sometimes roughened along interlobe sinuses, glabrous on both surfaces. Petals 6, glabrous, 1.2–1.4 × 1–1.2 cm, white flushed with pink unilaterally, obovate, apically rounded, entire. Stamens 12, free and declined to one side of the flower opposing the style; filaments 5–6 mm long; anthers 3.5–5 mm long, 1 mm wide, yellow, linear-oblong and tipped with a solitary, dorsally-inclined pore; connective modified dorso-basally into a deflexed spur 0.25 mm long. Ovary 1/2-inferior, 4-locular, glabrous at the apex but not elevated into a cone or collar. Style declinate and sigmoid, glabrous, 10–11 mm long; stigma punctiform. Berry 7–10 × 10 mm. Seeds clavate to narrowly pyriform or pyramidate, 1 mm long.

DISTRIBUTION AND PHENOLOGY. — Local and uncommon in cloud forests from the Boquete region of W Panama (Chiriquí) to the Fortuna Dam region and E to Cerro Colorado at 1000–1300 m. Flowering and fruiting material has been collected in January, March, April, and July.

REPRESENTATIVE SPECIMENS EXAMINED. — Chiriquí: Edwin Fabrega Dam and Reserve along trail to Río Hornito above Los Planes, 8°45'N, 82°15'W, 18 Jan. 1989, *Almeda et al.* 6309 (CAS, MO, PMA); Monte Rey, above Boquete, 21 Jul. 1971, *Croat & Porter* 15692 (CAS, MO). Chiriquí/Bocas del Toro border; windswept cloud forest off the road to Cerro Colorado, 26 Jan. 1989, *Almeda et al.* 6418 (CAS, CR, DUKE, MO, PMA, US).

DISCUSSION. — The outstanding features of *T. fragrantissima* are its completely glabrous leaves with closely spaced (0.25 mm) transverse secondary veins on abaxial foliar surfaces, linear-oblong anthers with solitary pores, and 4-locular ovary. Live flowers of this species produce a pleasant perfume-like fragrance, but nothing is known about its role in attracting pollinators. For illustrations of this species see Almeda (1990:319) and Plate 1.

10. *Topobea gerardoana* Almeda, sp. nov. (Fig. 3)

TYPE. — COSTA RICA. Limón. Cordillera de Talamanca between Quebrada Kuisa and Río Lari, 09°20'25"N, 83°13'45"W, elev. 2100 m, 17 Mar. 1993, *Herrera* 5914 (holotype: CAS!: isotypes: CR, INB!, MO).

Frutex epiphyticus. Petioli 1.5–3.6 cm longi; lamina 6–12.5 × 2.1–5.5 cm elliptico-obovata vel elliptica apice acuminata basi acuta, supra glabra, subtus sicut ramuli sparsiuscule pilis induti, 3–5-plinervata, nervis secundariis 1–3 mm inter se distantibus. Flores 6-meri in quoque nodo superiore singuli vel bini, pedunculis 1.3–2 cm longis; bracteae exteriores 7–8 × 5–6 mm ovatae vel elliptico-ovatae ca. 2–3 mm coalitae apice acuto vel rotundato; bracteae interiores 6–7 × 6 mm omnino liberae. Calycis tubus 0.5–0.75 mm longus, lobis 5 mm longis. Petala alba, 1–1.2 × 0.8–1 cm obovata apice mucronato. Filamenta 3–3.5 mm longa; antherae 3 × 1 mm inter se non cohaerentes, poro unico dorsaliter inclinato; connectivum ad basim dorsaliter dente 0.25 mm longo descendenti armatum. Stylus 1–1.1 cm; ovarium 6-loculare et 2/3 inferum apice glabro (cono ca. 1 mm alto).

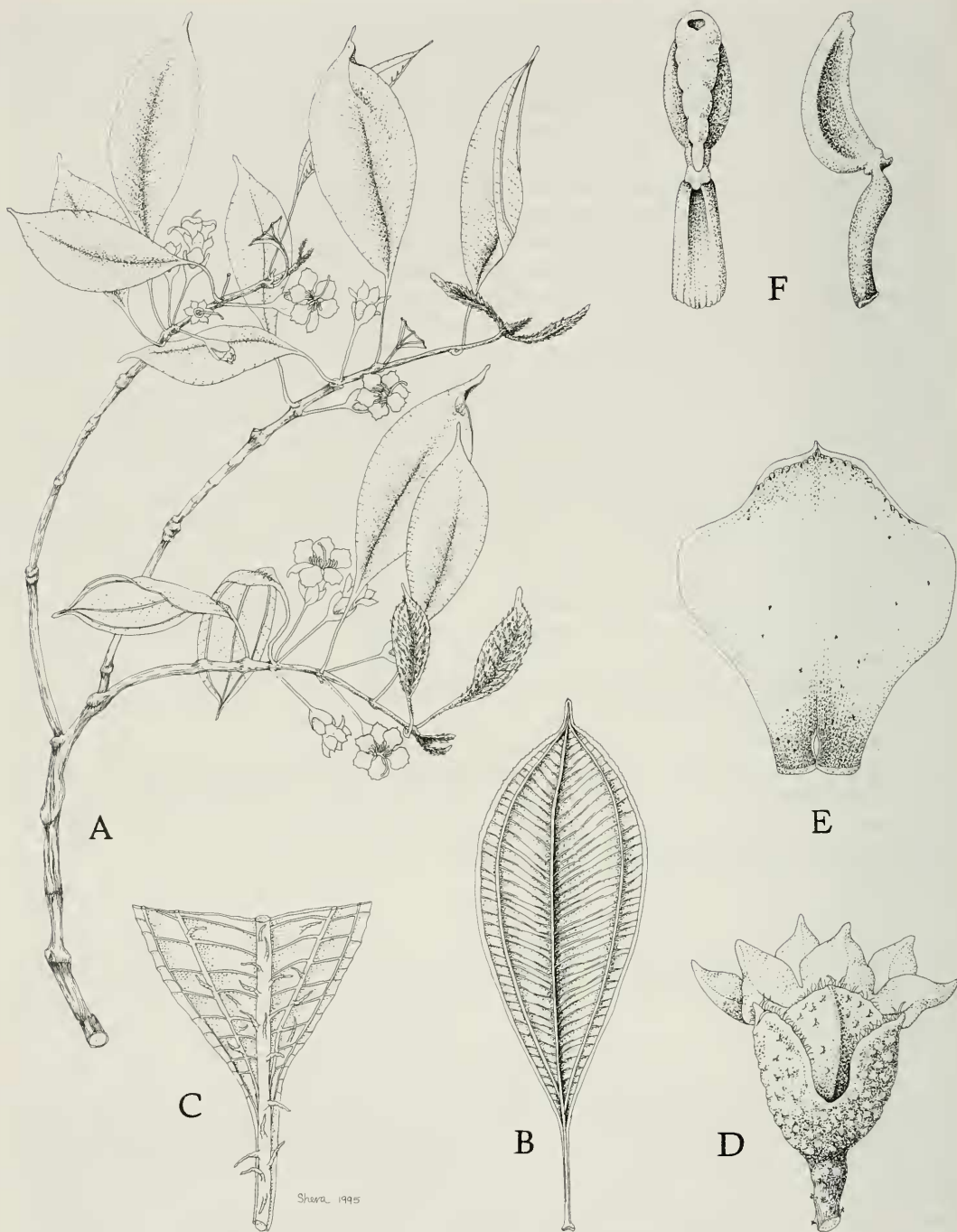


FIGURE 3. *Topobea gerardoana* Almeda. A. habit, ca. 1/3; B. representative leaf (abaxial surface), 3/5; C. enlarged leaf base (abaxial surface) showing indument detail, ca. 1; D. young fruiting hypanthium with decussate floral bracts, 3; E. petal (adaxial surface), 4; F. stamens, dorsal view (left) and profile view (right), ca. 7. (A-F from Herrera 5914.)

Epiphytic shrub. Uppermost internodes, vegetative buds, and abaxial surfaces of some mature leaves sparingly covered with a caducous indument of rusty brown subulate and conic hairs. Mature leaves of a pair mostly unequal in size; petioles 1.5–3.6 cm long; mature blades subcoriaceous, 6–12.5 cm long and 2.1–5.5 cm wide, elliptic-obovate to elliptic, the apex acuminate, the base acute, the margin entire to obscurely denticulate, 3–5-plinerved with the innermost pair of primary veins diverging from the median vein 1–5 mm above the blade base, the subparallel secondary veins spaced 1–3 mm apart at the widest portion of the blade. Flowers erect, solitary or paired in leaf axils of uppermost branches; peduncles 1.3–2 cm long, subquadrate and lenticellate. Floral bracts entire, glabrate or sparingly covered abaxially with a lanate indument, the margins ciliate or fimbriate; outer bracts 7–8 × 5–6 mm, fused at the base for 2–3 mm, concave, ovate to elliptic-ovate, the apex bluntly acute to ± rounded; inner bracts 6–7 × 6 mm, free, oblong to oblong-ovate, the apex rounded. Hypanthium (in young fruit) suburceolate. Calyx tube 0.5–0.75 mm long; calyx lobes (in young fruit) erect, 5 mm long and 3 mm wide at the base, triangular, irregularly and sparingly covered with a caducous lanate indument on both surfaces. Petals 6, 1–1.2 × 0.8–1 cm, white, obovate, apex mucronate, entire. Stamens 12; filaments 3–3.5 × 1.5 mm, complanate, glabrous and tapering to the apex; anthers 3 mm long and 1 mm wide, free, yellow, oblong and somewhat sickle-shaped in profile view with a solitary dorsally declined apical pore; connective thickened dorsally and modified dorso-basally into an appendage 0.25 mm long or less. Ovary 2/3-inferior, 6-locular, apex glabrous and elevated into a blunt cone about 1 mm high. Style straight, glabrous, 1–1.1 cm long; stigma punctiform. Immature berry 8 × 7–8 mm. Seeds narrowly pyriform, 1 mm long, tan with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Presently known only from cloud forests in southeastern Costa Rica in a region upslope and south of the Valle de Talamanca at 1900–2100 m. The two known collections were made in March. One is in flower, the other is in young fruit.

PARATYPE. — COSTA RICA. Limón: Cantón de Talamanca. Bratsi, Amubri, Alto Lari, Kivut. Ridge between Río Lari and Río Dapari, 9°22'45"N, 83°06'15"W, 25 Mar. 1992, *Herrera 5492* (CAS, INB).

DISCUSSION. — This little-known Costa Rican endemic has well-defined triangular calyx lobes that are irregularly and sparingly covered with a caducous lanate indument (Fig. 3D), free anther thecae that are somewhat sickle-shaped in profile view with a solitary apical pore (Fig. 3F), and an anther connective that is modified dorso-basally into an appendage 0.25 mm long or less. *Topobea gerardoana* does not appear to be particularly close to any congener with single-pored anthers.

ETYMOLOGY. — This species is named for Gerardo Herrera, stellar collector of Costa Rican plants.

11. *Topobea intricata* Almeda, *Brittonia* 53:157. 2001.

TYPE: COSTA RICA. Cartago: Highway #224 on property of ICE hydroelectric plant (now Tapantí National Park) ca. 20–24 km E of the church in Orosí, elev. 1500–1800 m, 5 Jan. 1974, *F. Almeda et al. 2366* (holotype: CAS!; isotypes: BM!, CR!, DUKE!, INB!, MEXU!, MO!, NY!).

Epiphytic or terrestrial shrub 1–2 m tall with spreading branches to 3 m long. Uppermost branchlets rounded. Cauline internodes, vegetative buds, leaf blades (both surfaces), peduncles, floral bracts, hypanthia, and calyx lobes moderately to copiously hirsute with smooth ferruginous hairs mostly 0.5–3(–6) mm long. Mature leaves of a pair typically unequal in size; blades thin and papery when dry, the larger one at each node 7.5–17.2 × 3.5–7.5 cm, the smaller one 1.8–10 × 1.7–5.4 cm, elliptic to elliptic-ovate, the apex acuminate to caudate-acuminate, the base obliquely obtuse to rounded, the margin denticulate to subentire (sometimes obscurely and remotely so), 3–5-plinerved with the innermost pair of primary veins diverging from the median vein 1–5 mm above the blade base, the transverse secondary veins spaced 2–6 mm apart at the widest portion of the blade. Flowers erect or

horizontally spreading, solitary in the axils of uppermost branches; peduncles 3.5–5.2 cm long, terete. Floral bracts green and entire; outer bracts $2.5\text{--}3.2 \times 1.7\text{--}2.6$ cm, free, ovate to subcordate, the apex acute to acuminate, trinerved; inner bracts $1.9\text{--}2.5 \times 0.7\text{--}1$ cm, the basal half closely appressed to but free from the hypanthium, narrowly elliptic-lanceolate, the apex acute to acuminate. Calyx lobes (at anthesis) linear oblong, 6–7 mm long and 1 mm wide at the \pm deltoid base between sinuses. Petals 6, glabrous, $1.6\text{--}2.3 \times 1.4\text{--}1.7$ cm, white flushed with pink distally on the abaxial surface, thin and translucent when dry, obovate, apex rounded, base somewhat clawed, entire. Stamens 12; filaments $5\text{--}6.5 \times 1$ mm, declinate, complanate, glabrous; anthers free, $5\text{--}7.5 \times 1$ mm, yellow, oblong-subulate and incurved distally, each with 2 confluent, dorsally-inclined pores at the truncate apex; connective thickened dorso-basally into a blunt deflexed appendage 0.5–1 mm long. Ovary 1/2-inferior (at anthesis), 6-locular, glabrous at the summit which is elevated into a lobulate collar 1–1.5 mm high surrounding the style base. Style glabrous, 0.9–1.4 cm long; stigma punctiform. Berry red at maturity, $1\text{--}1.7 \times 1.3\text{--}1.4$ cm. Seeds mostly 1 mm long, beige, cuneate to narrowly pyriform.

DISTRIBUTION AND PHENOLOGY. — Locally common in cloud forests of Tapantí National Park in central Costa Rica and the Fortuna region of western Panama at 1100–1800 m. Collected in flower from December through June, in fruit from March through July.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Cartago: About 15 km S of Tapantí along new road on the E slope above the Río Grande de Orosí near the concrete bridge, $9^{\circ}42'N$, $83^{\circ}47'W$, 12–17 Dec. 1969, *Burger & Liesner 6810* (CAS, CR, F); Cantón de Paraiso, Parque Nacional Tapantí, Valle de Reventazón, Sendero Arboles Caidos, $09^{\circ}45'00''N$, $83^{\circ}47'00''W$, 21 July 1994, *Quesada 123* (INB). PANAMA. Bocas del Toro: Fortuna Dam area, along continental divide trail bordering Chiriquí Province, $08^{\circ}45'04''N$, $82^{\circ}15'04''W$, 10 Mar. 1988, *Almeda et al. 6048* (BM, CAS, CR, MEXU, MO, NY, PMA); 2 km W of continental divide along trail to elfin forest, $08^{\circ}47'N$, $82^{\circ}13'W$, 26 Mar. 1985, *Hampshire & Whitefoord 981* (BM, CAS). Chiriquí: Fortuna Dam area, trail to meteorological station of Río Hornito, $08^{\circ}45'N$, $82^{\circ}18'W$, 23 June 1994, *Croat & Zhu 76310* (CAS, MO); Fortuna Dam area, road from Gualaca to Chiriquí Grande on continental divide trail W of road, $08^{\circ}45'N$, $82^{\circ}15'W$, 18 Jan. 1986, *de Nevers & McPherson 6852* (CAS, MO); Road from Fortuna Lake to Chiriquí Grande on trail W of continental divide, $08^{\circ}47'N$, $82^{\circ}13'W$, 22 Mar. 1985, *Hampshire & Whitefoord 850* (BM); Cordillera Central, 7 Dec. 1996, *Montenegro 1585* (CAS, SCZ); Distrito Boquete, Fortuna Dam site along trail following continental divide, 8 Feb. 1985, *van der Werff & van Hardeveld 6707* (CAS, MO).

DISCUSSION. — *Topobea intricata* has a copious cover of ferruginous hairs throughout, thin papery leaves, solitary floral peduncles, and ovate to subcordate outer floral bracts. It most closely resembles *T. dimorphophylla* in habit, pubescence details, leaf morphology, and petal color. For a comparison of these two species see the discussion under the latter. *Topobea intricata* is also superficially similar to *Blakea wilburiana* Almeda of central Panama. The latter has elliptic-lanceolate outer floral bracts, filiform to nearly acicular calyx lobes, and smaller anthers ($4\text{--}5 \times 1\text{--}2$ mm) that are oblong and laterally compressed with ventrally-inclined (vs. dorsally-inclined) apical pores.

As noted in the protologue, what may be a regional variant or a closely related undescribed taxon, represented by *Herrera 6036* (CAS, INB) and *Herrera 2832* (CAS), has been collected on the Caribbean slopes of the Cordillera de Talamanca in southern Costa Rica. This entity, which is known from five gatherings, is similar to *T. intricata* in all details but has outer floral bracts that are uniformly elliptic and consistently smaller ($1.3\text{--}1.5 \times 0.8\text{--}1.5$ cm). The known collections of *T. intricata* from geographically distant areas in Costa Rica and Panama are homogeneous morphologically. It is for this reason that I am reluctant to consider this distinctive population a mere variant without additional study. See Almeda (2001:158) for an illustration of this species.

12. *Topobea laevigata* (D. Don) Naudin, *Ann. Sci. Nat. Bot.* 3, 18:150. 1852.

Blakea laevigata D. Don, *Mem. Wern. Nat. Hist. Soc.* 4:327. 1823. TYPE. — MEXICO, without exact locality, Sessé & Mociño *s.n.* (BM! ex Herb. Lambert).

Epiphytic shrub or tree 5–10 m tall with a lateral spread of up to 8 m. Uppermost branchlets rounded-quadrate becoming rounded with age, essentially glabrous throughout, the young floral buds and peduncles sometimes covered with a caducous furfuraceous indument of stellulate or amorphous branlike hairs. Mature leaves of a pair equal to slightly unequal in size; petioles 0.8–3.4 cm long; blades coriaceous, 3.6–18 × 1.8–7.3 cm, elliptic to elliptic-obovate, the apex acuminate to abruptly short-acuminate, the base acute to obtuse, the margin entire, 3–5-nerved with the marginal pair of veins obscure or lacking or 3–5-plinerved with the inner pair of primary veins diverging from the median vein 4–7 mm above the blade base (on abaxial surface), commonly with some leaves bearing slitlike pit domatia at the abaxial margin of the blade near the petiole-laminar junction, the transverse secondary veins often obscure or 0.5–1 mm apart at the widest portion of the blade when visible. Flowers erect, solitary or in clusters of 2–4 in each leaf axil of distal branches; peduncles 1.2–2 cm long. Floral bracts glabrous at maturity, ± rigid, concave, and tightly enveloping the hypanthium; outer bracts 4.5–5 × 6–7 mm, fused basally for 2–4 mm or sometimes essentially free to the base, broadly deltoid to oblate or semicircular; inner bracts 4–5–6 mm, free, semicircular. Hypanthium (at anthesis) campanulate, 5–6 × 6–7 mm. Calyx tube 2.5 mm long, erect and cupulate, calyx broadly flattened into low undulations 0.5 × 3 mm. Petals 6, glabrous, 1.3 × 0.4–0.5 cm, white, narrowly obovate. Stamens 12; filaments 4–5.5 mm long, declinate, complanate, glabrous; anthers free, 4.5–5 × 1 mm, yellow, each with 2 confluent, dorsally-inclined pores at the emarginate apex; connective thickened dorsally, unappendaged or with a blunt dorso-basal callosity. Ovary 1/2-inferior, 6-locular, elevated apically into a low flangelike rim that forms a wide circle around the stylar scar. Style glabrous, 1.2–1.3 cm long; stigma punctiform. Berry 6–7 × 6 mm. Seeds ovoid to ± pyriform, 1 mm long, beige with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Local in montane rainforests, seasonal evergreen forests and oak-pine forests from southern Mexico (Pueblo and Veracruz, southward) to Guatemala and Belize at 300–1850 m. Flowering collections have been made in January, April, July, September, October, and December, fruiting collections have been gathered in every month except July and September.

REPRESENTATIVE SPECIMENS EXAMINED. — BELIZE. Toledo: high ridge, Jacinto Creek, Río Grande, 28 Oct 1944, *Gentle 4928* (CAS, LL). GUATEMALA. Alta Verapaz: Sebol, in potrero, 21 Apr. 1964, *Contreras 4440* (DS). Izabal: El Estor, in high forest, *Contreras 11464* (CAS). Peten: La Cumbre, top of hill in zapotal, on Pusila Road, 5 km north, *Lundell & Contreras 20228* (CAS, LL). MEXICO. Chiapas: Municipio of Berriozabal, 13 km N of Berriozabal near Pozo Turipache and Finca El Suspiro, 25 Dec. 1972, *Breedlove & Thorne 30771* (DS); Municipio of Cintalapa, between Colonia Francisco I. Madero and Colonia A. Lopez Mateos, 29 Mar. 1981, *Breedlove 50564* (CAS); Municipio of La Trinitaria, 10 km ENE of Dos Lagos above Santa Elena, 19 Jan. 1982, *Breedlove & Almeda 57558* (CAS); Municipio of Ocosingo, adjacent to Laguna Ocotal Grande, 6 Feb. 1973, *Breedlove 33070* (DS); Municipio of Peltalcingo, steep slope of Ahk'ulbal Nab above Peltalcingo, 28 Mar. 1981, *Breedlove 50424* (CAS). Oaxaca: Municipio San Miguel Chimalapa. Cerro Salomon ca. 2 km en línea recta al NNO del Cerro Guayahitos, ca. 43 km en línea recta al N de San Pedro Tapantepec, 23 Dec. 1985, *Wendt et al. 5156* (CAS). Puebla: Municipio Eloxochitlan, adelante de San Miguel Eloxochitlan en camino hacia El Mirador, 12 June 1985 *Chazaro & Leach 3392* (CAS). Veracruz: Municipio Hidalgotitlan. Afluente del Río Las Cuevas, ± 5 horas a pie al S de la Laguna, 16 Apr. 1982, *Wendt et al. 3845* (CAS).

DISCUSSION. — When present in a species of *Topobea*, acarodomatia are commonly produced with consistency on most leaves of all individual plants. In *T. laevigata*, the production of domatia is inconsistent. In the specimens examined for this study, no foliar domatia were found in collections from Belize and Guatemala. Among Mexican collections studied, domatia were observed as follows: Chiapas—some leaves on 18 of 20 collections; Oaxaca—some leaves on two of five collections; Puebla—some leaves on the single collection studied; Veracruz—some leaves on three of four collections examined. For differences between *T. laevigata* and *T. calycularis* see the discussion under the latter.

13. *Topobea lentii* Almeda, Brittonia 53:160. 2001.

TYPE: COSTA RICA. Cartago: 3 km E of Cachi, beside Rio Naranjo, 1300 m, 11 July 1971, *Lent 2000* (holotype: MO!; isotypes: BM!, CR!, F!, DUKE!, PMA!, US!).

Epiphytic shrub. Uppermost branchlets bluntly quadrate with elevated internodal lines or ridges but becoming rounded and coarsely striate with age. Young vegetative buds, floral peduncles, young floral bracts, hypanthia, and calyx lobes moderately covered with a caducous indument of scurfy and/or stellulate hairs. Mature leaves of a pair equal to somewhat unequal in size, essentially glabrous on both surfaces; blades coriaceous, 4.2–9.1 cm long and 1.9–4.3 cm wide, elliptic to elliptic-ovate, the apex bluntly acuminate, the base acute to obtuse, the margin entire, 5-plinerved, the innermost primaries diverging from the median vein 2–6 mm above the blade base (on abaxial surface) and forming plicate acarodomatia sparsely to moderately covered with barbellate hairs in the angles formed with the median vein, the transverse secondary veins spaced 0.25 mm apart at the widest portion of the blade. Flowers erect, 2–5 per axil in uppermost leafy branches; peduncles 5–7 mm long, lenticellate. Floral bracts free, sometimes recurved at the apex; outer bracts 3–3.5 × 2–2.5 mm, elliptic-ovate, the apex bluntly acute to rounded; inner bracts 2–2.5 × 2–2.5 mm, elliptic to elliptic-ovate, the apex rounded. Calyx tube 1.5–2 mm long, cupulate; free portions of calyx lobes 0.5–1.5 mm long and 0.5–1.5 mm wide basally between sinuses, broadly subtruncate and often apiculate, somewhat callose-thickened at the median apex abaxially. Petals 6, glabrous but sometimes fringed with inconspicuous caducous white hairs, 6–6.5 × 2–3 mm, reportedly white (fide *Lent 2000*) or pink (fide *Haber ex Bello 5174*), obovate-rhombic, the apex bluntly long-acuminate and somewhat concave. Stamens 12; filaments 3 mm long, somewhat declinate, complanate, glabrous; anthers free or laterally connate (in part), 2.5 mm long, 0.25 mm wide, pale yellow (?) and granulose along the lower ventral half of the thecae, subulate, each with a solitary, dorsally-inclined apical pore; connective thickened dorso-basally and prolonged near the filament insertion into a deflexed caudiform appendage 0.5 mm long. Ovary 1/2 inferior, 6-locular, glabrous and elevated at the apex into a lobulate collar 1 mm high that surrounds the style base. Style glabrous, 5–7 mm long; stigma punctiform. Berry 3–7 × 2.5–7 mm. Seeds 0.75–1 mm long, beige, cuneate to obovoid or narrowly pyriform.

DISTRIBUTION AND PHENOLOGY. — A rare cloud forest epiphyte known only from the vicinity of Cachi in central Costa Rica and the Río Chiquito de Tilarán in Guanacaste province at 1300–1450 m. Collected in flower in July and December, in fruit in July.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Cartago: pasture on hilltop, 2 km E of Cachi, 9°49'N, 83°47'W, 16 Dec. 1972, *Lent 3118* (F, US). Guanacaste: Río Chiquito de Tilarán, Río Negro, 10°22'N, 84°52'W, 1 July 1986, *Haber ex Bello 5174* (CAS).

DISCUSSION. — Notable features of *T. lentii* are its hair tuft foliar domatia, small fruiting hypanthia, clawed obovate-rhombic petals, ventro-basally granulose anther thecae, and dorso-basal caudiform appendages on anther connectives. It most closely resembles the widespread *T. watsonii* which differs in its well-defined triangular calyx lobes, larger petals (10–16 × 4.5–7 mm), longer an-

ther thecae (6–7.5 mm) that are connate for a major portion of their length, and the absence of foliar domatia. See Almeda (2001:161) for an illustration of this species.

14. *Topobea maurofernandeziana* Cogn., DC. Monogr. Phan. 7:1193. 1891.

TYPE. — COSTA RICA. Forêts de Juan Viñas, 25 Jan. 1890, *Tonduz 1844* (holotype: BR!; isotype: CR!).

Topobea durandiana Cogn., Bull. Soc. Roy. Bot. Belgique Ser. 3, 30:268. 1892. TYPE. — COSTA RICA. Bord d'un torrent a Buenos Aires, 250 m, 11. 1891, *Pittier 3789* (holotype: BR!).

Blakea intercepta Gleason, in Woodson & Schery, Ann. Missouri Bot. Gard. 28:435. 1941. TYPE. — COSTA RICA, without exact locality, 20 June 1874, *O. Kuntze s.n.* (holotype: NY!).

Terrestrial or epiphytic shrub 2–5 m tall and 3–7 m in diameter. Uppermost cauline internodes quadrate. Uppermost internodes, young vegetative and floral buds, and petioles sparsely to densely furfuraceous pubescent but glabrate with age. Leaves thick and coriaceous when dry; petioles 1.8–9 cm long; blades 11.5–23 × 7–18.5 cm, elliptic to elliptic-oblong or ovate, the apex abruptly acuminate, the base obtuse to rounded, the margin entire, 5-nerved or 5-plinerved, adaxially glabrous, sparingly furfuraceous to almost glabrous abaxially. Flowers 2–5 (rarely solitary) in each leaf axil of upper branchlets; peduncles 0.6–2.5 cm long. Inner and outer floral bracts 0.7–1.2 × 0.7–1.5 cm, essentially free, ovate to suborbicular, the apex rounded to retuse or obscurely apiculate. Calyx tube (on fruiting hypanthia) 0.6–0.8 cm long from the torus; free portions of calyx lobes 1 × 5 mm, broadly depressed-truncate with an apiculate callosity at the median apex, margin ± entire. Petals 6, glabrous, 1.7–2.5 × 1–1.3 cm, pink, obovate, the apex rounded to obliquely subtruncate. Stamens 12; filaments 7–9 mm long, declinate; anthers laterally connate, 6–9 × 1–2 mm, pink or yellow flushed with pink or red distally, linear-oblong and incurved distally, each with 2 confluent, dorsally-inclined apical pores; connective prolonged dorso-basally into a caudiform appendage 1 mm long. Ovary 1/3 inferior, 6-locular, the apex covered with a caducous ring of minute glandular hairs surrounding the styler scar. Style glabrous, 1.2–1.5 cm long; stigma truncate to capitate. Berry 1–1.4 × 1.3–1.5 cm. Seeds 1 mm long, beige, cuneate to clavate.

DISTRIBUTION AND PHENOLOGY. — Locally common in rainforests and cloud forests, often on remnant pasture trees from southern Mexico (Guerrero and Oaxaca) disjunct to Nicaragua, Costa Rica, and Panama from sea level to 1600 m. Flowering collections have been made from September through July, fruiting collections from February through November.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela: about 2–4 km N of Bijagua on road to Upala, 1 Mar. 1978, *Almeda & Nakai 4041* (CAS, CR). Cartago: about 3 km E of Cachi, 24 Jul. 1977, *Almeda et al. 3209* (CAS, CR). Guanacaste: Parque Nacional Guanacaste, Estación Cacao, Liberia, 10°55'45"N, 85°28'15"W, 2 Nov. 1990, *Chavez 339* (CAS, CR, INB, MO). Heredia: Parque Nacional Braulio Carrillo, Estación Magsasay. Sarapiquí, 10°24'10"N, 84°03'30"W, 4 Apr. 1991, *Aguilar 126* (CAS, CR, INB, MO). Limón: Parque Nacional Tortuguero, Estación Cuatro Esquinas. Laguna Tortuguero, 10°32'02"N, 83°30'26"W, 4 Jul. 1990, *Chavarria 116* (CAS, CR, INB, MO). Puntarenas: Las Cruces Tropical Botanical Garden and vicinity about 6.4 km S of San Vito de Java, 18 Mar. 1978, *Almeda et al. 4273* (CAS, CR). San José: Reserva Biológica Carara. Sitio El Chuzazo, 9°45'05"N, 84°31'50"W, 14 Feb. 1990, *Ziñiga 110* (CAS, CR, INB, MO). MEXICO. Guerrero: Sierra Madre Sur. Along road between El Paraíso and Puerto del Gallo, 6–8.7 miles NE of El Paraíso, 9 Mar. 1987, *Daniel & Bartholomew 4932* (CAS). Oaxaca: Distrito de Putla, La Cascada, 5 km al NE de La Hacienda, sobre al camino San Vicente-San Isidro, 13 Apr. 1987, *Garcia et al. 3171* (CAS). NICARAGUA. Chontales: vicinity of Finca San Pedro de Oluma, on NE flanks of Cerro Oluma, 12°18'N, 85°23'W, 22 Sep. 1983, *Nee 28328* (CAS).

Matagalpa: falda norte del Cerro Musún, frente a trocha a Wanawás, 16 May 1980, *Araquistain & Moreno 2798* (CAS). Río San Juan: near Caño Chontaleño, 20 km NE of El Castillo, 18–21 Apr. 1978, *Neill & Vincelli 3560* (CAS). Zelaya: NW de Estación Experimental El Recreo, 12°10'N, 84°18'W, 2 May 1982, *Sandino 2702* (CAS). PANAMA. Chiriquí: 15–20 km S of Volcán, road to Barrilos, 22 Dec. 1974, *Dressler 4903* (CAS).

DISCUSSION. — This is one of the most common species of *Topobea* in lowland sites of southern Central America. Like *T. watsonii*, the only notable variation in this species is in the amount and persistence of the indument on upper internodes, vegetative and floral buds, petioles and peduncles. In the protologue of *T. durandiana*, which was published shortly after *T. maurofernandeziana*, Cogniaux gives no specific differences that can be used to separate these two species. Judging from the species descriptions it appears that Cogniaux assigned those collections with furfureaceous-puberulent petioles and peduncles to *T. durandiana* whereas collections from the glabrous end of the spectrum were recognized as *T. maurofernandeziana*.

Blakea intercepta is also included here in synonymy with confidence. The holotype consists of three leaves and many young fruits. Although petals and anthers are lacking, the available material is an exact match for *T. maurofernandeziana*.

15. *Topobea mcphersonii* Almeda, *Brittonia* 53:163. 2001.

TYPE: PANAMA. Comarca de San Blas: San Blas boundary trail on Llano-Cartí road, 9°15'N, 79°00'W, elev. ca. 350 m, 27 Jan. 1986, *McPherson & Merello 8176* (holotype: CAS!; isotypes: BM, CR, EAP, MEXU, MO, PMA, US).

Epiphytic shrub. Uppermost branchlets bluntly quadrate becoming rounded with age. Young vegetative buds covered with an amorphous lanate indument. Mature leaves of a pair equal to slightly unequal in size, glabrous on both surfaces but glandular-punctate abaxially; petioles 0.5–1.2 cm long; blades coriaceous, 4.1–7.5 cm long and 1.7–3 cm wide, elliptic-obovate to obovate, the apex bluntly cuspidate, the base acuminate, the margin entire, 3–5-plinerved, the marginal pair of primaries inconspicuous and concealed by the revolute margins when dry, the transverse secondary veins spaced 0.5–1 mm apart at the widest portion of the blade. Flowers erect, solitary in leaf axils of uppermost branches; peduncles 1.2–2 cm long. Floral bracts green flushed with red, entire and glabrous throughout; outer bracts 1.6–2.1 × 1–1.6 cm, free but conspicuously decurrent on and imparting a winged aspect to the the peduncle, elliptic to elliptic-obovate, apex bluntly cuspidate to bluntly acute; inner bracts 1.1–1.5 × 0.3–0.6 cm, free, linear-oblong to narrowly obovate and distinctly cucullate, apex bluntly acute to obtuse. Calyx tube 2 mm long; free portions of calyx lobes 0.5–1 mm long and 3–4 mm wide basally between sinuses, broadly depressed-triangular, margin entire, callose-thickened at the median apex abaxially, glabrous throughout. Petals 6, glabrous, 2.1–2.7 × 1.2–1.5 cm, reportedly white-pink, thin and translucent when dry, obovate, apically rounded, entire. Stamens 12; isomorphic, filaments 5–6 mm long, declinate, complanate, glabrous; anthers laterally connate for most of their length, 3–5 mm long, 1 mm wide, yellow, linear-oblong with each anther sac opening by a separate, dorsally-inclined terminal pore; connective thickened dorsally and dilated dorso-basally into an upturned or deflexed somewhat flattened, blunt appendage ca. 0.5 × 0.25 mm. Ovary completely inferior, 6-locular, glabrous at the apex which is elevated into a blunt cone 1–3 mm high. Style and stigma not seen. Berry subglobose, 0.6–0.7 × 0.7 cm. Seeds mostly 1 mm long, beige, cuneate-clavate.

DISTRIBUTION AND PHENOLOGY. — A lowland rainforest species known only from El Llano-Cartí region of north-central Panama at 100–500 m. Collected in flower and fruit in January and February.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Comarca de San Blas: Río Nergala, 9°22'N, 79°7'W, 12 Jan. 1985, *de Nevers & Herrera 4530* (CAS, MO). Panamá: 14 km above Panamerican Highway on road from El Llano to Carti-Tupile, 20 Feb. 1973 (fr), *Kennedy 2502* (MO, US).

DISCUSSION. — *Topobea mcphersonii* is unlike other described congeners in having floral bracts that are prominently decurrent on the floral peduncles. The inner floral bracts, which are oblong and do not tightly envelop the hypanthia, are also distinctive as are the laterally connate anther thecae with cleft or divergent pores and upturned or deflexed staminal appendages. Because of these unique features, the relationships of this species are obscure at this time. For an illustration of this species see Almeda (2001:164).

16. *Topobea multiflora* (D. Don) Triana, Trans. Linn. Soc. London 28:149. 1871. (Fig. 4)

Blakea multiflora D. Don, Mem. Wern. Nat. Hist. Soc. 4:326. 1823. (Fig. 4) TYPE. — PERU. Without exact locality: *Pavón 127-3* (holotype: K!, fragment at BR!).

Epiphytic shrub 2–4 m tall or free standing tree to 8 m tall. Uppermost branchlets quadrate becoming somewhat striate and rounded with age, the younger nodes covered with caudate-acuminate stipuliform flaps ca. 3 mm long that envelop caducous tufts of hair, the distal portions of each flap \pm caducous with age and leaving a prominent interpetiolar ridge or corky line. Vegetative and young floral buds, calyx lobes (in bud), peduncles, and young pedicels moderately to sparsely covered with a caducous indument of amorphous scurfy hairs. Mature leaves of a pair essentially equal in size, glabrous on both surfaces at maturity; petioles 1.4–6 cm long; blades coriaceous, 10.3–18.5 \times 6–10.4 cm, elliptic, the apex abruptly acuminate, the base acute, the margin entire, 5-nerved or 5-plinerved with the innermost primaries diverging from the median vein ca. 5 mm above the blade base (on abaxial surface) with hair tuft acarodomatia that are sparsely to moderately covered with robust shaggy hairs (0.5–2 mm long) in the angles formed with the median vein, the transverse secondary veins spaced 0.25–1.5 mm apart at the widest portion of the blade. Flowers erect, borne in clusters of (1–) 2–6 in each leaf axil of distal branches; peduncles 0.3–2.1 cm long. Floral bracts essentially glabrous at maturity and closely enveloping the hypanthium; outer bracts 5–8 \times 5–7 mm, fused basally for 4–6 mm, broadly ovate to suborbicular, the free distal portion bluntly acute to broadly rounded; inner bracts 7–9 \times 10–11 mm, free but imbricate, obdeltoid to suborbicular, often appearing \pm rounded due to the firm concave posture. Hypanthium (at anthesis) campanulate, 7–8 \times 5–6 mm. Calyx tube 4–6 mm long, erect and cupulate; calyx subtruncate or barely evident as broadly oblate apiculate lobes 0.5–4–5 mm. Petals 6, glabrous, 1.1–1.8 \times 0.5–1.2 cm, pink with a translucent whitish inverted V-shaped lens at the base of each petal, narrowly obovate to spatulate, the apex bluntly acute to \pm rounded, margin entire but inconspicuously caducous-fimbriate. Stamens 12; filaments 9 mm long, declinate, complanate, glabrous; anthers laterally connate for at least half their length, 6–9 \times 1 mm, yellow, oblong-subulate, each with 2 confluent, dorsally-inclined apical pores; connective thickened dorsally and prolonged dorso-basally into a deflexed toothlike appendage 0.5–2.5 mm long. Ovary 1/4-inferior, 6-locular, elevated apically into a glabrous cone 3 mm high and a lobulate collar ca. 1 mm long. Style glabrous, 1.3–1.5 cm long; stigma \pm truncate to somewhat expanded. Mature berry and seeds not seen.

DISTRIBUTION AND PHENOLOGY. — Locally common in rainforest habitats from central Costa Rica to Panama, Ecuador, Peru, and Bolivia from sea level to 1400 m. Flowering has been recorded from November through July; fruiting collections have been made in February and March and from May through July.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela: Reserva Forestal de San Ramón, 10°12'53"N, 84°36'28"W, 28 Jan. 1987, *Herrera & Solis 457* (CAS, CR, MO). Puntarenas:

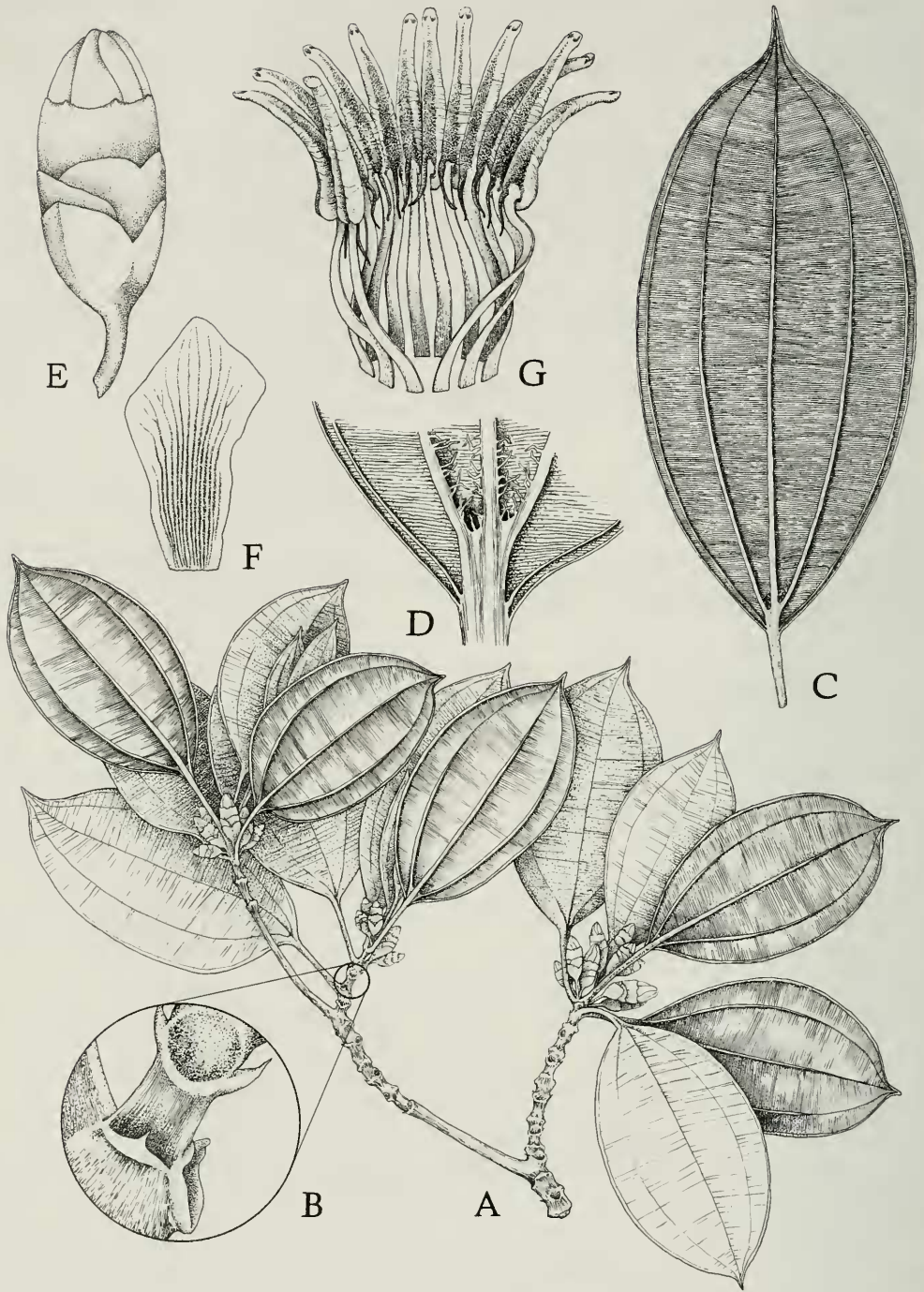


FIGURE 4. *Topobea multiflora* (D. Don) Triana. A. habit, 1/5; B. nodal enlargement showing stipuliform flaps. ca. 3; C. representative leaf (abaxial surface), ca. 1/2; D. enlarged leaf base (abaxial surface) showing hair tuft acarodomatia, ca. 3; E. flower bud with enveloping bracts, ca. 3; F. petal (adaxial surface), ca. 3; G. androecium, ca. 3. (A, B from McPherson 7630; C, D from McPherson 15046; E-G from Almeda et al. 4271 and McPherson 7964.)

Las Cruces Tropical Botanical Garden and vicinity about 6.4 km S of San Vito de Java, 18 Mar. 1978, *Almeda et al.* 4271 (CAS, CR). San José: about 13–18 km S of San Isidro del General, 5 Mar. 1978, *Almeda & Nakai* 4105 (CAS, CR, INB, MBM). PANAMA. Coclé: ca. 9 km beyond the market in El Valle de Antón on a rock road to trail head to Cerro Caracoral, 16 Feb. 1996, *Almeda et al.* 7600 (CAS, PMA); along Llano Grande to Coclesito road above Cascajal, near divide, 8°42'N, 80°28'W, 11 Jan. 1986, *McPherson* 7964 (CAS, MO, PMA); near El Valle de Antón, 8°37'N, 80°07'W, 25 Nov. 1985, *McPherson* 7630 (CAS, MO, PMA). Colón: Río Guanache, 1–4 km upstream from Portobelo Road, 10 Dec. 1973, *Gentry* 8767 (MO). Darién: Alturas de Nique on the Serranía de Pirre above the Cana mining camp, 1 Mar. 1988, *Almeda & McPherson* 5967 (CAS, PMA); Cana region on trail above Cana leading to ridge of Pirre massif, 7°45'N, 77°45'W, 5 May 1990, *McPherson* 15046 (CAS, MO, PMA). Panamá: road past Altos de Pacora, 3–3.5 miles NE of Altos de Pacora, 11.1–11.6 miles beyond Lago Cerro Azul, 9°15'N, 79°25'W, 19 June 1988, *Croat* 68669 (CAS, MO, PMA).

DISCUSSION. — This frequently collected species is recognized by a combination of characters that includes stipuliform nodal flaps on uppermost branches (Fig. 4B), hair tuft domatia on abaxial foliar surfaces (Fig. 4D), laterally connate anther thecae, and dorso-basal toothlike appendages on anther connectives (Fig. 4G). In the past, Central American collections of *T. multiflora* have been erroneously identified as *T. calycularis*. Standley (1938), for example, reported it from Costa Rica (as *T. calycularis*) based on collections from Cañas Gordas made in 1897 (*Pittier* 10955 and *Pittier* 11062, both at US). It was not reported for Panama by Gleason (1958) because the species had not yet been collected in that country. *Topobea calycularis* is presently known only from Mexico (Chiapas) and adjacent Guatemala. Like *T. multiflora*, it also has hair tuft foliar domatia but it has free anther thecae that are essentially unappendaged, a 4-locular ovary, and lacks stipuliform nodal flaps.

For the most part, Central American material of *T. multiflora* has modally shorter floral peduncles (0.3–2.1 cm vs. 2–3 cm) than South American populations. Cogniaux was aware of this difference and may have intended to give formal taxonomic recognition to the Central American populations because he annotated at least one Costa Rican collection (*Pittier* 10955, BR) as *T. multiflora* var. *brevipedunculata*. The fact that this infraspecific epithet was never published also suggests that he may have changed his mind. I see no compelling reason for recognizing such an entity.

17. *Topobea parasitica* Aubl., *Hist. Pl. Guiane Fr.* 1:476. 1775.

TYPE. — FRENCH GUIANA. Sinnemary River, *Aublet s.n.* (holotype: BM!).

Topobea regeliana Cogn., DC. Monogr. Phan. 7:1085. 1891. TYPE. — PANAMA. Chagres, Isthmus of Panama, Mar. 1850, *Fendler* 295 (holotype: LE: isotypes, BM!, BR! [2 sheets], K!, MO!, US!).

Topobea praecox Gleason, *Phytologia* 3:355. 1950. TYPE. — PANAMA. Coclé: El Valle de Antón, vicinity of La Mesa, *Allen* 2788 (holotype: NY!; isotypes: NY! [2 sheets]).

Topobea membranacea Wurdack, *Brittonia* 9:108. 1957. TYPE. — COLOMBIA. Antioquia: Anori-Cruces road, 11 May 1944, *Core* 677 (holotype: US!; isotype: NY!).

Robust shrub or small tree 2–10 m tall, often epiphytic or rupicolous. Uppermost branchlets bluntly quadrate becoming rounded with age. Juvenile vegetative buds and uppermost nodes covered with smooth stramineous hairs and a dense cover of stellulate or scurfy hairs. Uppermost cauline internodes, petioles, peduncles, abaxial leaf surfaces (especially elevated primary veins), outer floral bracts, and calyx lobes (in bud) moderately to sparsely covered with a varying mixture of scurfy, stellulate, and roughened hairs that fall away to varying degrees with age. Mature leaves of a pair somewhat unequal in size, glabrous on the adaxial surface at maturity, sparingly covered with scurfy or stellulate hairs to nearly glabrous on the abaxial surface at maturity; petioles 1.8–9 cm long; blades membranaceous to subcoriaceous, 6.2–25.5 × 5–16 cm, elliptic varying to elliptic-ovate, the apex

abruptly short-acuminate, the base obtuse to broadly rounded but sometimes varying to acute, the margin typically entire, rarely varying to denticulate, (5-)7(-9)-nerved with secondary veins spaced 1-4 mm apart at the widest portion of the blade, or 5-7-plinerved in some plants and then the inner pair of primary veins diverging 0.5-1 cm above the blade base (on abaxial surface). Flowers erect, 1-7 per leaf axil of uppermost branches; peduncles 0.3-1.9 cm long. Floral bracts free but appressed to and commonly obscuring the hypanthium below the calyx; outer bracts 5-10 × 5-9 mm, broadly ovate to subrotund, the apex typically rounded but varying to broadly obtuse, bluntly acute, acuminate or somewhat emarginate; inner bracts 5-9 × 5-9 mm, ovate to subrotund, the apex typically broadly rounded. Hypanthium (post anthesis) campanulate, 5-8 × 6-8 mm. Calyx tube 2-4 mm long, erect and cupulate; free portions of calyx lobes 1-2 long and 3-4 mm wide basally between interlobe sinuses, triangular varying to broadly depressed-triangular to nearly undulate in fruit. Petals 6, glabrous, 1.4-2 × 0.7-1.1 cm, reportedly pink, reddish-pink, or magenta, obovate, the apex rounded to obtuse. Stamens 12; filaments 9-12 mm long, declinate, complanate, glabrous; anthers laterally connate for about ¾ their length, 7-12 × 0.75-1 mm, pale yellow to cream-colored, subulate, each with 2 confluent, dorsally-inclined apical pores; connective thickened dorsally and prolonged dorso-basally into an acute spur 1-2 mm long. Ovary superior or 1/4- to 1/5-inferior, glabrous, 6-locular, elevated apically into a cone about 2 mm high and a shallow collar ca. 0.5 mm high, the latter disappearing as the ovary cone enlarges with age on mature fruits. Style glabrous, 1.2-1.4 cm long; stigma ± truncate but not conspicuously expanded. Berry becoming red at maturity on some plants, 6-9 × 7-8 mm. Seeds 1 mm long, tan, narrowly ovoid.

DISTRIBUTION AND PHENOLOGY. — Locally common in rainforests from central Costa Rica south through Panama to eastern Colombia and southeastern Venezuela, east to Surinam and French Guiana and south to the Brazilian Amazon (Amapá, Pará, Amazonas) from sea level to 1375 m. Flowering material has been collected from March through August, October and December, fruiting collections have been gathered from March through December.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela: between Cataratas and San Lorenzo about 13-17 km N of La Balsa de San Ramón, 8 June 1976, *Utley & Utley 5109* (CAS, DUKE). Puntarenas: ca. 1.1 km N of Las Cruces Tropical Botanical Garden on road to San Vito, 14 July 1977, *Almeda et al. 3058* (CAS, CR). San José: Reserva Biológica Carara Estación Bijagual, 9°46'N, 84°36'W, 23 Jul. 1990, *Bello 2357* (CAS, INB, MO). PANAMA: Canal Area: Pipeline Road, approx. 15 km N of Gamboa, 8 Oct. 1982, *Schmalzel & Moreno 1100* (CAS). Chiriquí: 7.5 miles from bridge over Río Chiriquí Viejo on road to Río Sereno, 7 Apr. 1979, *Hammel et al. 6877* (CAS, MO, PMA). Coclé: La Mesa at El Valle de Antón, 6.4 km along La Mesa road from El Valle main road, 28 Apr. 1977, *Folsom & Butcher 2834* (CAS, MO). Colón: upstream from bridge over Río Guanche, 27 May 1980, *Antonio 4793* (CAS, MO). Comarca de San Blas: Río Playón Chico, 09°13.5'N, 78°15'W, 8 June 1994, *Herrera et al. 1586* (CAS, MO). Darién: S of Garachiné on W slope of Serranía Sapo, above place called Casa Vieja, 25 May 1991, *McPherson et al. 15377* (CAS, MO, PMA). Herrera: W of Las Minas, on Montoso de Chepo, vicinity of Chepo, 07°42'N, 80°51'W, 20 May 1987, *McPherson 10931* (CAS, MO, PMA). Los Santos: Los Taretos, 10 Aug. 1962, *Dwyer 2432* (MO). Panamá: El Llano-Cartí highway, about 10 km N of El Llano, 20 Apr. 1973, *Dressler 4360* (MO).

DISCUSSION. — The *T. parasitica* complex, as interpreted here, is defined by a number of consistent qualitative characters. These include floral bracts that are free to the base, anther thecae that are laterally connate for about ¾ their length, spurlike dorso-basal anther appendages, a 6-locular ovary, and a superior or nearly superior ovary. The morphology of hair types comprising the indument is also diagnostic but indument presence and abundance vary considerably from population to population. Perhaps because of its comparatively widespread geographical distribution and elevational range, *T. parasitica* presents some puzzling variation in characters that are typically constant in other species. The most conspicuous variation involves leaf size and thickness, petiole length, number of flowers per leaf axil, peduncle length, floral bract size, calyx lobe development, hypanthial length, flower size,

and petal color. Extreme expressions for all of these characters are impressive. Previous students of the Melastomataceae who worked with geographically defined representatives of *Topobea* have seized on some of these differences in describing new taxa. When a large number of collections are examined from across the range of this species, however, it becomes clear that much of the character variation noted above is continuous or insignificant for the recognition of meaningful taxa. Gleason (1958), in his treatment of Melastomataceae for Flora of Panama, recognized *T. membranacea*, *T. praecox*, and *T. regeliana*, all of which I here relegate to the synonymy of *T. parasitica*, the oldest name applicable to this complex. Gleason used the name *T. praecox* for plants with triangular-ovate calyx lobes and flowers appearing when the leaves are lacking or at least not fully expanded. He described *T. membranacea* and *T. regeliana* as having calyx lobes that are almost obsolete and flowers appearing while the leaves are fully expanded. Gleason further differentiated these two species by the following couplet:

Leaves thinly coriaceous, flowers 1–2 per axil on pedicels 3–6 mm long *T. regeliana*
 Leaves membranaceous; flowers 4–6 per leaf axil on pedicels 10–15 mm long *T. membranacea*

Unfortunately most collections attributable to this complex are in fruit, so it is difficult to critically evaluate degree of leaf maturation with flowers at anthesis. Nevertheless, the taxonomic utility of this purported correlation seems dubious. All of the other characters that Gleason used to distinguish these three taxa are too variable or exhibit much overlap. Thus the character correlations used to differentiate what he interpreted as three species make little sense when applied to the many more collections now available for study from Central America. Because of this, I see no recourse other than to recognize *T. parasitica* as a variable complex with some modally extreme character combinations that break down as sample size increases.

In his treatment of *T. parasitica* for the Flora of the Guianas, Wurdack (1993) notes that other perhaps synonymous taxa in this complex include *T. rupicola* Hoehne of Brazil and *T. floribunda* Gleason and *T. rhodantha* Uribe of Colombia. For illustrations of *T. parasitica* see Gleason (1958:246) and Wurdack (1993:299).

18. *Topobea parvifolia* (Gleason) Almeda, Proc. Calif. Acad. Sci. 46:322. 1990.

Blakea parvifolia Gleason, Phytologia 3:357. 1950. TYPE. — PANAMA. Coclé: crest of Cerro Pajita, El Valle de Antón, 1100 m, Allen 3761 (holotype: NY!; isotype: MO!).

Tree 3–10 m tall. Uppermost branchlets glabrous, quadrisulcate but becoming rounded-quadrate with age. Young vegetative buds and floral peduncles sparingly covered with a caducous scurfy indument. Mature leaves of a pair essentially equal in size, adaxially glabrous, abaxially glandular-lepidote; petioles 0.6–1.4 cm long; blades coriaceous, 2.5–4.7 cm long and 1.4–2.6 cm wide, elliptic to obovate, the apex rounded to a blunt apiculum, the base acute to cuneate, the margin entire, 3–5-nerved with inconspicuous pustulate swellings that become perforated domatia at the abaxial blade base in the angles between the median vein and each of the two proximal lateral veins, the transverse secondary veins spaced 0.5–1 mm apart at the widest portion of the blade. Flowers erect, solitary in uppermost leaf axils; peduncles 1.7–3.1 cm long. Floral bracts free and entire; outer bracts 3.5–1.5–2 mm, narrowly ovate to ovate-lanceolate, apex rounded; inner bracts 3 × 1.5–2 mm, oblong, apex rounded. Calyx tube (fruiting hypanthia) 0.5–0.75 mm long, campanulate to cupulate; free portions of calyx lobes 0.75–1 mm long and 1.5–2 mm wide basally between interlobe sinuses, broadly triangular and often becoming bluntly apiculate on the most mature berries. Petals 6, obovate, glabrous with an irregular scattering of hyaline disc-shaped glands when dry, 0.7–1 × 0.5–0.6 cm, white or white flushed with pink along the margins. Stamens 12; filaments 2.5 mm long, declinate, gla-

brous; anthers oblong, laterally connate in a semicircular ring, 2–2.5 mm long, 0.5 mm wide, each anther sac opening by a separate dorsally inclined terminal pore; connective simple. Ovary 2/3-inferior, 4-locular, glabrous at the apex which is elevated into a low truncate cone that becomes increasingly rounded in fruit. Style glabrous, 6.5 mm long; stigma punctiform. Berry 6–6.5 × 6–6.5 mm. Seeds 1 mm long, beige, cuneate-clavate to narrowly pyriform.

DISTRIBUTION AND PHENOLOGY. — Locally common in ridgetop elfin forest on Cerro Pajita, Cerro Gaital, and vicinity in central Panama at 900–1100 m. Flowering has been recorded in November and December, February, and July, fruiting collections have been made in February and July.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Coclé: Cerro Gaital, east slope and ridges leading to the summit, 24 Feb. 1988, *Almeda et al.* 5898 (CAS, PMA); vicinity of La Mesa, beyond El Valle, on eastern ridge along trail to summit of Cerro Gaital, 08°37'N, 80°07'W, 13 July 1987, *McPherson 11261* (CAS, MO, PMA).

DISCUSSION. — This Panamanian endemic is known only from windswept slopes and ridges in the vicinity of El Valle de Antón. Among the species with small glabrous leaf blades and free floral bracts, *T. parvifolia* stands out by its inconspicuous pustulate swellings that become perforated domatia at the abaxial blade base in the angles between the median vein and each of the two proximal lateral veins. The anther thecae are unappendaged, laterally connate in a semicircular ring with each anther sac opening by a separate terminal pore, and the ovary is 4-locular.

19. *Topobea pittieri* Cogn., DC. Monogr. Phan. 7:1088. 1891.

TYPE. — COSTA RICA. La Palma, alt. 1550 m, 18 Dec. 1888, *Pittier 706* (holotype: BR!; isotypes: BR!, CR!).

Terrestrial or epiphytic shrub 1–4 m tall. Uppermost branchlets obscurely rounded-quadrate becoming rounded with age. Young internodes, young vegetative buds, bracts, hypanthia and calyx lobes sparsely to moderately squamulose with inconspicuous scales that may superficially appear like sessile glands. Mature leaves of a pair equal to slightly unequal in size; petioles 1.1–2.7 cm long; blades subcoriaceous, 6.5–14.5 × 2.6–7.5 cm, elliptic, the apex acuminate to caudate-acuminate, the base acute to obtuse and somewhat decurrent on the petiole, the margin obscurely undulate-crenulate, 5-plinerved with an additional inconspicuous intramarginal pair, the innermost primary veins diverging from the median vein 0.3–1 cm above the blade base (on abaxial surface) with pocket domatia formed where innermost primaries diverge from the median vein, the transverse secondary veins spaced 0.5–1.5 mm apart at the widest portion of the blade. Flowers erect, borne in clusters of 2 to 5 in each leaf axil of distal branches; peduncles 1–2.5 cm long. Floral bracts free and much shorter than the hypanthium and calyx; outer bracts 1.5–2.5 × 1.5–2.5 mm, ovate to deltoid; inner bracts 1–1.5 × 1.2–1.5 mm, broadly ovate to suborbicular. Hypanthium (at anthesis) narrowly campanulate, 3–3.5 × 3–3.5 mm. Calyx tube 1 mm long; calyx lobes 0.5–2–3 mm, truncate to retuse with inframarginal teeth positioned medially on the abaxial surface. Petals 6, glabrous, 7–8.5 × 3.5–4.5 mm, white or greenish-white, oblong-ovate and acute apically. Stamens 12; filaments 2.5–3.5 mm long, declinate and glabrous; anthers free, 2.5–3 × 0.5 mm, yellow, subulate, each opening by a solitary, dorsally-inclined pore; connective thickened dorsally and prolonged dorso-basally into a ± horizontal toothlike appendage 0.5 mm long. Ovary 3/4-inferior, 4-locular, slightly elevated at the summit into a low glabrous laterally lobulate blunt cone surrounding the stylar scar. Style glabrous, 5–8 mm long, stigma punctiform. Berry 5–9 × 6–8 mm, pink-purple at maturity. Seeds narrowly ovoid to cuneate, 1 mm long, deep purple with a smooth testa.

DISTRIBUTION AND PHENOLOGY. — Locally common in very wet cloud forests from Costa Rica south to Colombia and Ecuador at 500–1800m. Flowering and fruiting specimens have been collected during every month of the year.

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela: about 9.7 km N of Los Angeles de San Ramón, 23 Feb. 1978, *Almeda & Nakai 3846* (CAS, CR). Cartago: Refugio Nacional de Fauna Silvestre Tapantí, 22 Mar. 1986, *Almeda et al. 5709* (CAS, CR). Heredia: 12–15 km SW of Horquetas; Finca Rara Avis, transect SE across Rara Avis boundary along Rio Sardinal to S corner of property on boundary with Braulio Carrillo Park, 10°20'N, 84°02'W; 20 Apr. 1988, *Hammel et al. 16701* (CAS, CR, INB, MO). Limón: Cantón de Talamanca, Parque Nacional Cordillera de Talamanca, Río Coén, entre Ujarrás y San José Cabécar, 09°24'20, 83°13'30"W, 3 Apr. 1993, *Herrera 6194* (CAS, CR, INB, MO). San José: ca. 21 km N of San Isidro de Coronado on lower W slopes of Volcán Irazú, 5 July 1977, *Almeda et al. 2918* (CAS, CR). PANAMA. Bocas del Toro; Edwin Fabrega Dam and Reserve in Fortuna along the Continental Divide trail, 12.9 km N of Sitio de Presa offices above the dam, 08°48'04"N, 82°15'04"W, 7 Feb. 1996, *Almeda et al. 7539* (CAS, PMA). Chiriquí: Fortuna Dam area about 3.7 km S of the Sitio de Presa offices. Trail through Quebrada Alemán, 9 Feb. 1996, *Almeda et al. 7553* (CAS, PMA); Cerro Colorado, Bocas Road, 17–18 Feb. 1977, *Folsom et al. 1770* (CAS).

DISCUSSION. — This species is distinguished by the combination of pocket domatia on abaxial foliar surfaces, solitary anther pores, apically acute petals, seeds that are deep purple at maturity, and a 4-locular ovary. Cogniaux (1891), Standley (1938), and Wurdack (1980) overlooked the presence of foliar domatia in this species. He described them as "inner primaries calloused at the base beneath."

20. *Topobea pluvialis* Standl., Field Mus. Nat. Hist., Bot. Ser. 22:162. 1940.

TYPE. — PANAMA. Darién: Chepigana District, crest of Cana-Cuasi trail, 15 Mar. 1960, *Terry & Terry 1560* (holotype: F!; isotype: MO!).

Reportedly a tree 4–6 m tall or an epiphytic shrub. Uppermost branchlets quadrate becoming rounded with age and irregularly inflated into clavate-thickened formicaria just below some nodes. Young vegetative buds and young floral peduncles caducously covered with a furfuraceous indument of minute branlike hairs, otherwise glabrous throughout. Mature leaves of a pair somewhat unequal in size, glabrous on both surfaces at maturity; petioles 1.3–2.5 cm long; blades coriaceous, 10–15.5 × 3.4–7.7 cm, elliptic-oblong to elliptic-obovate, the apex caudate-acuminate, the base acute to obtuse, the margin entire, 5-plinerved with innermost primaries diverging from the median vein 3–9 mm above the blade base (on abaxial surface) and with hair tuft domatia that are sparsely covered with barbellate hairs in the angles formed with the median vein, the transverse secondary veins spaced 0.5–1.5 mm apart at the widest portion of the blade. Flowers erect, solitary or borne in clusters of 2–3 in each leaf axil of distal branches; peduncles 0.8–1.7 cm long. Floral bracts essentially glabrous at maturity; outer bracts 4–7 × 4 mm, free, ovate to elliptic-lanceolate; inner bracts 3–4 × 3–4 mm, free, depressed-ovate to suborbicular. Hypanthium cupulate, 5–6 × 6 mm. Calyx tube 2.5–3 mm long, erect; calyx with broadly depressed rounded-triangular lobes 1 × 3 mm, each of which is terminated by a tooth 0.5 mm high or the calyx often appearing nearly truncate. Petals 6, glabrous, 1–1.3 × 0.7–0.9 cm, white or pink (fide *Hartman 12381*), obovate, the apex bluntly acute to subrotund, the margin entire. Stamens 12; filaments 6–7 mm long, declinate, complanate, glabrous; anthers laterally coherent for about 2/3 of their length, 4–5 × 0.75 mm, yellow, oblong to oblong-subulate, each with 2 confluent, dorsally-inclined apical pores; connective somewhat thickened dorsally and prolonged dorso-basally into a deflexed tooth-like appendage 0.5–1 mm long. Ovary 1/3-inferior, 6-locular, elevated apically in a short stipe (0.5 mm high) bearing the stylar scar but lacking a collar. Style glabrous, 1.3–1.4 cm long; stigma ± conic when expanded. Immature berry 6 × 4 mm. Seeds mostly 1 mm long, beige, the testa smooth.

DISTRIBUTION AND PHENOLOGY. — A rare and little-collected species of the rainforests of southern Panama near the Colombian frontier at 900–1650 m. Flowering collections have been made in December and February through April, fruiting collections in April, November and December.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Darién: top of ridge leading to Cerro Pirre, near Rancho Plastico, 13 Nov. 1977, *Folsom et al.* 6282 (CAS, MO); SW ridge leading to Alturas de Nique, on border with Colombia, 29 Dec. 1980, *Hartman* 12381 (CAS, MO, PMA); Parque Nacional Darién, Cerro Pirre, 7 Feb. 1991, *Herrera et al.* 886 (CAS, MO).

DISCUSSION. — The foliar acarodomatia of *T. pluvialis* take the form of invaginated depressions on the abaxial surface but they are inflated and paired on the adaxial surface. These domatia are lacking in *T. inflata* Triana, a closely related Colombian species. This latter species also has fusiform internodal swellings (presumably inhabited by ants) that are larger and more consistently developed on uppermost internodes than in *T. pluvialis*. *Herrera et al.* 1485 (CAS) from San Blas, Panama (350–480 m) could represent an outlying population of *T. pluvialis* or a closely related taxon but it is in young bud and has abaxial foliar domatia that appear to be ruptured and devoid of hairs rather than open and covered with a few barbellate hairs. Better material is needed before this entity can be identified with certainty. *Topobea pluvialis* is the only known member of the genus in Mesoamerica that produces both cauline formicaria (presumably for ants) and foliar domatia for mites.

21. *Topobea standleyi* L. O. Williams, Fieldiana, Bot. 29:583. 1963.

TYPE. — GUATEMALA. Baja Verapaz: dry rocky hills in forest of pine and oak, north of Santa Rosa, 30 Mar. 1939, *Standley* 69709 (holotype: F!; isotype: NY).

Reportedly a terrestrial shrub or tree to 8 m tall. Uppermost branchlets ± terete, the very young internodes, vegetative buds, petioles on young leaves, floral peduncles, and abaxial leaf surfaces moderately furfuraceous with caducous branlike or stellulate hairs. Mature leaves of a pair somewhat unequal in size, glabrous on the adaxial surface at maturity; petioles 0.5–4 cm long; blades ± coriaceous, 9.5–15 × 5–10 cm, elliptic to elliptic-ovate, the apex abruptly acuminate, the base acute, the margin entire, 5-nerved (the outermost pair often obscure), the transverse secondary veins spaced 0.5–1 mm apart at the widest portion of the blade. Flowers erect, solitary or paired in each leaf axil of upper branches; peduncles 0.7–1.2 cm long. Floral bracts moderately to sparsely covered with a lanuginose indument of caducous matted hairs at maturity; outer bracts 6–8 × 5 mm, free, ovate, typically with a keeled median vein; inner bracts 5–6 × 5 mm, free, suborbicular to obovate. Hypanthium cupulate, 0.7–0.8 × 0.7 cm (at anthesis). Calyx tube 2.5 mm long, erect; calyx lobes bluntly deltoid and ± rounded apically (often appearing like erect blunt teeth on fruiting hypanthia), 1.5–2 × 2 mm, covered with a brown lanuginose indument of woolly matted hairs. Petals 6, glabrous, 0.7–1.1 × 0.5–0.9 cm, pink and white (fide *Standley* 69709), obovate, the margin obscurely retrorse-ciliolate. Stamens 12; filaments 5 mm long, declinate, complanate, glabrous; anthers free, 5.5–7 × 1 mm, oblong, each with 2 divergent, dorsally-inclined apical pores; connective somewhat thickened dorsally but not elaborated into an appendage. Ovary 1/2-inferior, 6-locular, the apex smooth, glabrous and lacking a cone and collar. Style glabrous, 9 mm long; stigma punctiform. Berry 8 × 5 mm. Seeds 1.5 mm long, beige with a black lateral raphe and smooth testa.

DISTRIBUTION AND PHENOLOGY. — Rocky hills in pine-oak forests of Central Guatemala at 1500 m. The two known collections, which are in flower and fruit, were collected in March and April.

REPRESENTATIVE SPECIMENS EXAMINED. — GUATEMALA. Baja Verapaz: pine-oak forest on rocky hills near and above Santa Rosa, 4 Apr. 1941, *Standley* 91045 (F, NY).

DISCUSSION. — This species, which has not been collected since April of 1941, appears to be a local endemic known only from the type and the one other collection cited above. It is readily recognized by its abruptly acuminate leaves, caducous lanuginose indument on hypanthia, calyx lobes, and

floral bracts, and unappendaged anthers, each of which has two divergent apical pores. For an illustration of this species see Standley and Williams (1963:520).

22. *Topobea suaveolens* Almeda, Proc. Calif. Acad. Sci. 46:323. 1990.

TYPE. — PANAMA. Veraguas: along trail to summit of Cerro Tute about ½ mile above the Escuela de Agricultura Alto Piedra near Santa Fe, 29 Jan. 1989, *Almeda et al.* 6484 (holotype: CAS!; isotypes: AAU!, BM!, BR!, CR!, DUKE!, F!, MEXU!, MICH!, MO!, NY!, PMA!, TEX!, US!).

Epiphytic tree to 4 m tall, often obscuring and overtaking the crowns of host trees. Uppermost branchlets quadrate to quadrisulcate and glabrous with well-defined interpetiolar ridges or lines. Vegetative buds caducously lepidote-furfuraceous. Mature leaves of a pair equal or slightly unequal in size, glabrous throughout; blades subcoriaceous, 3.6–5.3 × 1.6–2.5 cm, elliptic, the apex acuminate to caudate-acuminate, the base acute, the margin entire, 3-plinerved with an additional inconspicuous pair of submarginal veins, transverse secondary veins spaced mostly 0.25 mm apart at the widest portion of the blade, pocket domatia typically formed abaxially in the angles between the median vein and the two proximal lateral veins. Flowers pendent and solitary in the leaf axils of uppermost branches; peduncles 2.3–3 cm long, glabrous. Floral bracts glabrous, entire; outer bracts 4.5–7.5 × 3–4 mm, elliptic to elliptic-ovate, apex bluntly acute to rounded; inner bracts 4–4.5 × 4 mm, ovate to suborbicular, apex broadly rounded. Calyx tube 1.5 mm long; calyx lobes 1 mm long and 4 mm wide basally, broadly ovate to deltoid-ovate with a blunt callose-thickened tooth on the abaxial apex of each lobe, margin entire, glabrous throughout. Petals 6, glabrous, connivent to somewhat imbricate and bell-like when fully expanded, 1.2–1.5 × 0.9–1.1 cm, white flushed with dark pink along a broad marginal band, obovate, apically rounded, entire. Stamens 12, free and encircling the exerted style; filaments glabrous, 2.5–3.5 mm long; anthers 2.5 mm long, 1 mm wide, yellow, laterally compressed, oblong in ventral view and narrowly ovoid in profile view with a shallow dorso-basal depression at the filament insertion, tipped with a solitary, dorsally-inclined pore 0.75 mm in diameter; connective unappendaged. Ovary 1/2-inferior, 6-locular, elevated at the glabrous apex into a smooth dome 1–1.5 mm high. Style straight, glabrous, 8.5–9 mm long; stigma truncate. Berry 5–6 × 6–7 mm. Seeds narrowly and irregularly pyriform, 0.75–1 mm long.

DISTRIBUTION AND PHENOLOGY. — Known only from the cloud forests of Cerro Tute in west-central Panama at 850–1100 m. The three known collections, all of which are in flower and fruit, were collected from January through March.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Veraguas: vicinity of Cerro Tute, along trail to summit, 08°30'N, 81°07'W, 19 Mar. 1987, *McPherson* 10654 (CAS, MO, PMA); near Cerro Tute-Arizona, above Santa Fe and Alto de Piedra, 8°30'N, 81°10'W, 5 Feb. 1988, *McPherson* 12043 (CAS, MO, PMA).

DISCUSSION. — This little-collected Panamanian endemic appears to be restricted to the slopes of Cerro Tute. It is unusual among congeners in having sweet-smelling flowers that are pendent with free connivent anthers that form a ring around the exerted style. *Topobea suaveolens* also has distinctive laterally compressed anthers that are uniporose and narrowly ovate in profile view with a conspicuous dorso-basal depression near the filament insertion. For an illustration of this species see Almeda (1990:324).

23. *Topobea tetramera* Almeda, sp. nov. (Fig. 5)

TYPE. — PANAMA. Veraguas: headwaters of Río Caloveborita ca. 15 km past Escuela Agrícola Alto Piedra above Santa Fé on the Atlantic watershed, 500 m, 16 May 1981, *Sytsma & Anderson* 4758 (holotype: CAS!; isotype: MO, PMA).

Frutex epiphyticus vel terrestris. Ramuli sicut pedunculi folia inflorescentia hypanthiaque pilis 1–2 mm longis induti. Folia in quoque pari dimorpha papyracea et denticulata. Folia maiora: lamina 4.5–9.4 × 2.3–4.3 cm elliptica vel elliptico-ovata vel elliptico-obovata apice acuminata basi asymmetricice obtusa vel rotundata 5-plinervata. Folia minora: lamina 0.7–1.7 × 0.6–1 cm ovata apice acuta basi obtusa vel rotundata 3-nervata. Flores 4-meri in quoque nodo superiori singuli; pedunculis 3–4 mm longis; bracteae omnino liberae 0.7 × 0.2–0.4 cm elliptica apice acuta; bracteae interiores omnino liberae 0.9 × 0.3–0.4 cm elliptica apice acuta vel acuminata. Calycis tubus 1 mm longus, lobis 0.7 × 0.2 cm. Petala 0.8–0.9 × 0.5–0.7 cm obovata. Antherarum thecae 2 × 0.75 mm inter se non cohaerentes, dorsaliter biporosae; connectivum nec prolongatum nec appendiculatum. Ovarium 4-loculare et omnino inferum, cono glabro (collo non evoluto).

Epiphytic or terrestrial shrub to 2 m tall. Uppermost branchlets quadrate becoming rounded with age. Cauline internodes, leaf blades (both surfaces), peduncles, floral bracts, hypanthia, and calyx lobes moderately to copiously hirsute with rusty brown hairs mostly 1–2 mm long. Mature leaves of a pair markedly unequal in size; blades coarsely papery when dry, the larger one at each node 4.5–9.4 × 2.3–4.3 cm, elliptic varying to elliptic-ovate or elliptic-obovate, the apex abruptly acuminate, the base somewhat obliquely obtuse to rounded, the margin denticulate (sometimes obscurely so), 5-plinerved with the innermost pair of primary veins diverging from the median vein 2–5 mm above the blade base, the transverse secondary veins spaced 2–4 mm apart at the widest portion of the blade; petiole 5–7 mm long; the smaller blade 0.7–1.7 × 0.6–1 cm, ovate, apex acute, base rounded to obtuse, margin entire, 3-nerved, the transverse secondary veins not evident; petiole 2–3 mm long. Flowers erect, solitary in each axil of uppermost leaves, peduncles 3–4 mm long. Floral bracts green and entire; outer bracts 0.7 × 0.2–0.4 cm, free, narrowly elliptic, apex acute; inner bracts 0.9–1 × 0.3–0.4 cm, free, narrowly elliptic, apex acute to acuminate. Hypanthium (at anthesis) 4 mm long to the torus and 4 mm in diameter. Calyx tube 1 mm long, erect or somewhat flaring at anthesis. Calyx lobes (at anthesis) 4, deltoid at the base but abruptly tapered to narrow linear segments 0.7 cm long and 0.2 cm wide at the base between sinuses. Petals 4, glabrous, 0.8–0.9 × 0.5–0.7 cm, translucent white (fide *de Nevers et al. 5460*) or translucent pink (fide *Sytsma & Andersson 4758*), thin and translucent when dry, obovate, the apex rounded, the base broadly clawed, entire. Stamens 8, isomorphic; filaments 3–3.5 × 0.5 mm, complanate, glabrous; anthers free, 2 × 0.75 mm, yellow, narrowly ovoid, each with 2 confluent, somewhat dorsally-inclined pores at the truncate apex; connective thickened dorsally but unappendaged. Ovary completely inferior (at anthesis), 4-locular, glabrous at the summit which is elevated into a blunt cone surrounding the stylar scar. Style glabrous, 5.5–6 mm long; stigma punctiform. Berry red at maturity, 6–8 × 7–8 mm. Seeds 1 mm long, white, narrowly pyriform to cuneate, testa smooth.

DISTRIBUTION AND PHENOLOGY. — Local and evidently uncommon in low rainforests from the Fortuna region of western Panama east to Cerro Brewster in central Panama at 800–1100 m. Collected in flower in April and May, in fruit in November.

ADDITIONAL SPECIMENS EXAMINED. — PANAMA. Chiriquí: Fortuna Dam area, along Quebrada Bonito to E of road, 8°45'N, 82°13'W, 8 Feb. 1984 (sterile), *Churchill et al. 4767* (MO). Comarca de San Blas: Cerro Brewster, premontane rain forest, 9°18'N, 79°16'W, 21 Apr. 1985, *de Nevers et al. 5460* (CAS); Cerro Brewster, premontane rain forest, 9°18'N, 79°16'W, 20 Nov. 1985, *de Nevers et al. 6266* (CAS). Veraguas: 11 km from Escuela Agrícola Alto de Piedra, along Río Dos Bocas, 15 Nov. 1974, *Mori & Kallunki 3092* (CAS, MO).

DISCUSSION. — This extraordinary species appears to be highly derived because of its 4-merous flowers (Fig. 5F) with eight stamens and a 4-locular ovary. The strongly dimorphic leaves at each node (Fig 5A) and the copious rusty brown hirsute pubescence on vegetative and floral parts are also characteristic. These latter features are shared with *T. dimorphophylla* which differs in having partly fused inner floral bracts, 6-merous flowers with 12 stamens, and a 6-locular ovary.

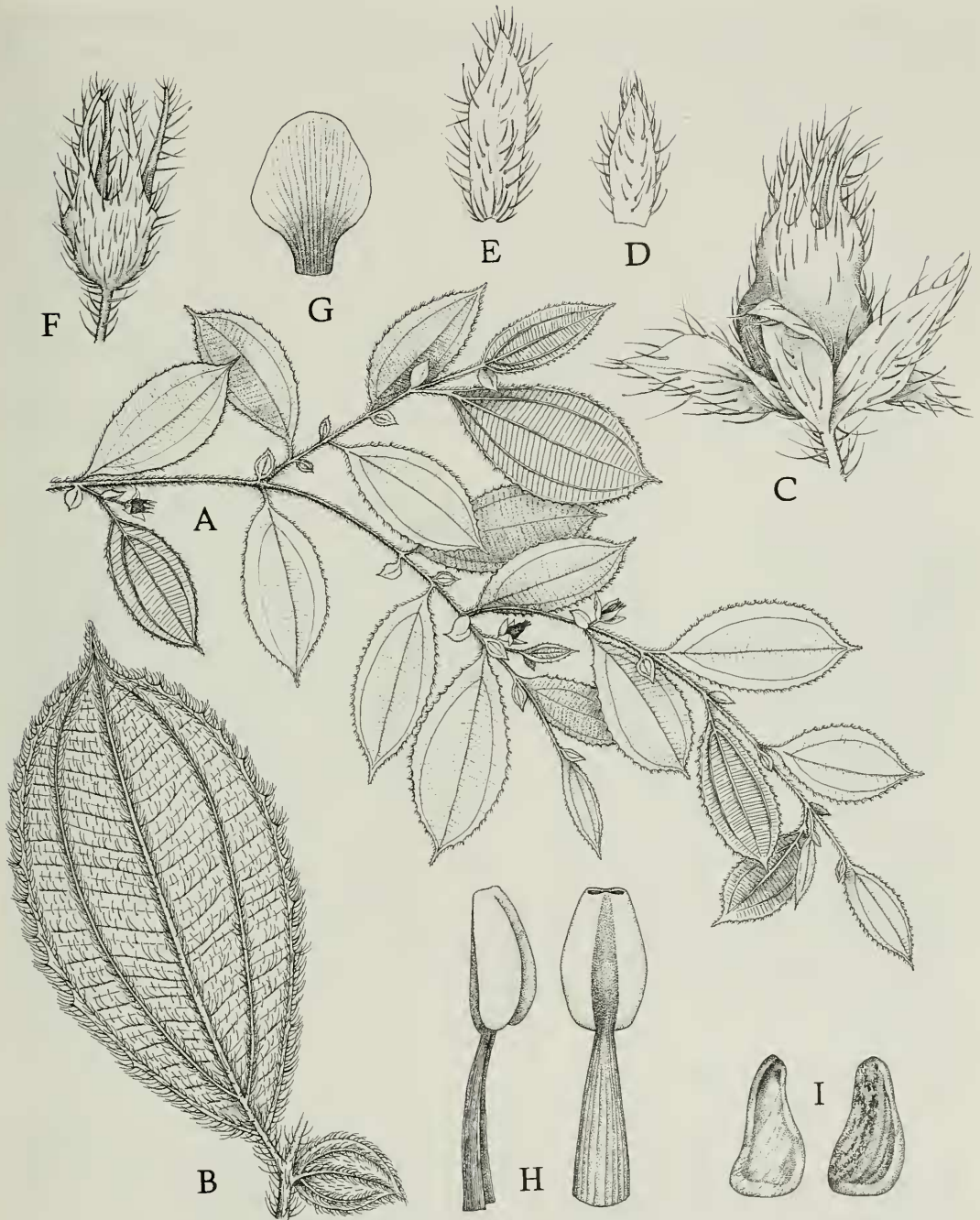


FIGURE 5. *Topobea tetramera* Almeda. A. habit, 1/5; B. foliar dimorphism at a node, ca. 1; C. fruiting hypanthium with attached decussate floral bracts, ca. 3; D. outer floral bract (adaxial surface), ca. 3; E. inner floral bract (adaxial surface), ca. 3; F. hypanthium (at anthesis) with floral bracts, petals, androecium, and style removed, ca. 3; G. petal (adaxial surface), ca. 3; H. stamens, 1/4 profile view (left) and dorsal view (right), 10; I. seeds, 20. (A, B from Mori & Kallunki 3092; C-I from Sytsma & Anderson 4758.)

ETYMOLOGY. — The epithet for this species is derived from the Greek words *tetra*, meaning four, and *merus*, referring to number of parts, in reference to the unusual 4-merous flowers and 4-locular ovary of this species.

24. *Topobea watsonii* Cogn., DC. Monogr. Phan. 7:1089. 1891.

TYPE. — GUATEMALA. Prope Chocon River, 11 Mar. 1885, *Watson 94/211* (holotype: BR!).

Topobea rosea Gleason, Publ. Carnegie Inst. Wash. 522: 536. 1940. TYPE. — BELIZE. Temash River, 13 Mar. 1936, *Schipp 1320* (holotype: NY!).

Topobea urophylla Standl., Field Mus. Nat. Hist., Bot. Ser. 22:162. 1940. TYPE. — PANAMA. Darién: Chepigana District, Río Balsa, above Tucutí, 6 Mar. 1940. *Terry & Terry 1411* (holotype: F!; isotype: MO!).

Topobea cooperi Gleason, Phytologia 3:354. 1950. TYPE. — PANAMA. Bocas del Toro: Cricamola Valley, Region of Almirante, Jan.–Mar. 1928, *Cooper 199* (holotype: NY!; isotype: F!).

Topobea allenii Standl. & L. O. Williams, Ceiba 3:216. 1953. TYPE. — COSTA RICA. Puntarenas: Esquinas Forest, region between Río Esquinas and Palmar Sur de Osa, alt. 75 m, 5 Feb. 1951, *Allen 5844* (holotype: EAP; isotypes: F!, US!).

Scandent epiphytic shrub with lax branches 3–4 m long. Uppermost branchlets bluntly quadrate but becoming rounded with age. Juvenile growth, uppermost cauline internodes, peduncles, and floral bracts moderately to densely covered with barbellate or stellulate and scurfy hairs but glabrate with age. Mature leaves of a pair equal to somewhat unequal in size, adaxially glabrous, abaxially sparsely covered with plumose or barbellate hairs (mostly on the elevated primary veins) and stellulate or branlike hairs (especially on the actual surface) varying to nearly glabrous; petioles 1–4.8 cm long; blades coriaceous, 5.5–16.5 × 3–7.7 cm, elliptic to elliptic-ovate, the apex long-acuminate to abruptly caudate, the base obtuse to rounded, margin entire, 3–5-nerved or 3–5-plinerved (sometimes with an intramarginal pair of obscure veins), the transverse secondary veins spaced 0.25–0.5 mm apart at the widest portion of the blade. Flowers erect, 1–4 per leaf axil of uppermost branches; peduncles 0.7–1.3 cm long. Floral bracts free or connate basally for 1–2 mm, elliptic to elliptic-ovate, apex acute to rounded apically; outer and inner bracts 0.6–1 × 0.4–0.8 cm. Calyx tube 3–4 mm long, campanulate; free portions of calyx lobes 2–3 mm long and 2.5–3.5 mm wide basally between interlobe sinuses, bluntly triangular with a prominently elevated callose-thickened tooth or appendage at the median apex abaxially. Petals 6, glabrous or stellulate puberulent abaxially, 10–16 × 4.5–7 mm, pink, rhombic-ovate to obovate, the apex ± acute. Stamens 12; filaments 5–7 mm long, declinate, complanate and glabrous; anthers laterally connate, 6–7.5 × 1 mm, yellow, granulose along lower ventral half of the thecae, each with 2 confluent, dorsally-inclined pores; connective prolonged dorso-basally into a deflexed caudiform appendage 0.5–1 mm long. Ovary 1/3-inferior, 6-locular, glabrous and elevated at the apex into a lobulate stylar collar 1–1.5 mm high. Style glabrous, 1.2–1.6 cm long; stigma capitellate. Berry red, 1–1.3 × 0.9–1.3 cm. Seeds 1–1.5 mm long, beige, narrowly ovoid to cuneate.

DISTRIBUTION AND PHENOLOGY. — Locally common in low rainforests and cloud forests from southern Mexico (Chiapas) and Belize south through Central America (excluding El Salvador) to Colombia from sea level to 1400 m. Flowering specimens have been collected from October through February and in May, fruiting collections from February through September.

REPRESENTATIVE SPECIMENS EXAMINED. — BELIZE. Toledo: Edwards Road beyond Columbia, on high ridge, 11 Nov. 1947, *Gentle 6316* (CAS, LL). COSTA RICA. Puntarenas: between Golfo Dulce and Río Térraba, Nov. 1947 (without exact date), *Skutch 5263* (US). GUATEMALA. Petén: Los Arcos, 2 km, E of Km 143 on Cadenas Road, 17 Dec. 1969, *Contreras 9379* (CAS, LL, US). Izabal: Río Chacón, 8 Feb. 1921, *Johnson 1237* (US). HONDURAS. Gracias a Dios: Ahuas Bila, 200 km SO de Puerto Lempira, orilla del Río Wankí, Coco o Segovia, 5–13 May 1985, *Nelson & Cruz*

9319 (CAS, TEFH). MEXICO. Chiapas: Municipio Las Margaritas, low ridges at the confluence of the Río Lacantum (Río Jataté) on the Guatemala border, 14 Mar. 1973, *Breedlove & McClintock 34103* (DS, MEXU). NICARAGUA. Jinotega: below Peñas Blancas via El Tuma, 6 May 1976, *Neill 253* (CAS, MO). Matagalpa: Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradon, ca. 13°14–15'N, 85°38'W, 20–21 Jan. 1982, *Stevens et al. 21282* (CAS, MO). Nueva Segovia: 10 km SE of Jalapa, 24 Dec. 1973, *Atwood et al. 6827a* (CAS, MO). Zelaya: along road from Bonanza (airstrip) through Constancia (mineshaft) to Laguna Siempreviva (dam), 23 Apr. 1978, *Stevens 8015* (CAS, MO). PANAMA. Bocas del Toro: Laguna de Chiriquí, 15 km oeste de Punta Cricamola, entrando Ensenada de Catavela, y subiendo Quebrada Nuri, 8°55'N, 81°49'W, 19 Mar. 1993, *Foster et al. 14602* (CAS, PMA). Coclé: Caribbean side of divide at El Copé, 8°35'W, 8°45'N, 4 Feb. 1983, *Hamilton & Davidse 2769* (CAS, MO, PMA). Colón: lumber road on Santa Rita east ridge, 23 Feb. 1968, *Correa & Dressler 748* (MO). Comarca de San Blas: trail from Puerto Obaldía inland towards Bongo, 24 Mar. 1985, *D'Arcy & McPherson 16142* (MO); Playón Chico, Río Ukupseni caminando por el Río Ukupseni, 09°15'N, 78°15'W, 30 Oct. 1991, *Herrera et al. 1024* (CAS, MO, PMA). Darién: Parque Nacional del Darién, ridge between N & S branches of Río Pucuro, across river from old Kuna village of Tacarcuna ca. 18 km E of Pucuro, 8°04'N, 77°16'W, 21 Oct. 1987, *Hammel et al. 16336* (CAS, MO, PMA). Panamá: along newly cut road from El Llano to Carti-Tupile, 12 miles above Pan-American highway, 13 Mar. 1973, *Croat 22899* (CAS).

DISCUSSION. — This species is defined by a number of diagnostic characters. The petals are rhombic-ovate to obovate and stellulate-puberulent abaxially (in part), the anthers are dorso-basally appendiculate, the thecae are laterally coherent for about 2/3 of their length and distinctly granulose along their lower ventral sides, and the ovary has a conspicuous fimbriate-lobulate styler collar. This comparatively widespread species is variable in the density and persistence of the indument on cauline internodes, peduncles, and floral bracts. It is otherwise uniform in all other diagnostic features. The types of *T. allenii*, *T. cooperi*, *T. rosea*, and *T. urophylla*, taxa here relegated to synonymy, are good matches for typical *T. watsonii* in all diagnostic features. When Standley and Williams described *T. allenii* from Costa Rica they suggested a relationship with *T. urophylla* which is understandable in view of the taxonomy adopted here. Gleason also appears to have been unaware of *T. watsonii* when he described *T. rosea* from Belize because he compared it only to *T. calycularis* in the protologue. In his treatment of *Topobea* for Flora of Panama, Gleason (1958) recognized only *T. cooperi* and *T. urophylla*. His key to the genus suggests that he maintained these species based on a sparse furfuraceous indument for the former and an indument of barbellate hairs for the latter. Specimens from throughout the range of this species often have varying combinations and densities of these two indument types making Gleason's purported distinctions taxonomically insignificant.

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LITERATURE CITED

- ALMEDA, F. 1984. New and noteworthy additions to the Melastomataceae of Panama. *Proc. Calif. Acad. Sci.* 43(17):269–282.
- . 1990. New species and new combinations in *Blakea* and *Topobea* (Melastomataceae), with an historical perspective on generic limits in the tribe Blakeeae. *Proc. Calif. Acad. Sci.* 46(14):299–326.
- . 2000a. The hexandrous species of *Topobea* (Melastomataceae). *Proc. Calif. Acad. Sci.* 52(9):97–109.
- . 2000b. A synopsis of the genus *Blakea* (Melastomataceae) in Mexico and Central America. *Novon* 10:299–319.
- . 2001. Three new Mesoamerican species of *Topobea* (Melastomataceae). *Brittonia* 53(1):157–166.
- COGNIAUX, C. A. 1891. Mélastomacées. In *Monographiae phanerogamarum*, A. and C. de Candolle, eds. 7:1–1256. G. Masson, Paris.
- GLEASON, H. A. 1939. The genus *Clidemia* in Mexico and Central America. *Brittonia* 3:97–140.
- . 1958. Melastomataceae. In *Flora of Panama*, R. E. Woodson, Jr. and R. W. Schery, eds. *Ann. Missouri Bot. Gard.* 45:203–304.
- LUMER, C. 2000. The reproductive biology of *Blakea* and *Topobea* (Melastomataceae). In *Monteverde: Ecology and conservation of a tropical cloud forest*, N. M. Nadkarni and N. T. Wheelwright, eds. Oxford University Press, Oxford.
- STANDLEY, P. C. 1924. Melastomaceae. In *Trees and shrubs of Mexico*. *Contr. U. S. Natl. Herb.* 23(4):1046–1074.
- . 1938. Melastomaceae. In *Flora of Costa Rica*. *Field. Mus. Nat. Hist., Bot. Ser.* 18(3):783–845.
- STANDLEY, P. C. AND L. O. WILLIAMS. 1963. Melastomaceae. In *Flora of Guatemala*. *Fieldiana, Bot.* 24:407–525.
- WALTER, D. E. AND H. C. PROCTOR. 1999. *Mites: Ecology, evolution and behaviour*. University of New South Wales Press Ltd., Sydney.
- WINKLER, S. 1965. Die Melastomataceae von El Salvador. *C. A. Bot. Jahrb. Syst.* 83:331–369.
- WURDACK, J. J. 1980. Melastomataceae. In *Flora of Ecuador*, G. Harling and B. Sparre, eds. 13:1–406.
- . 1993. Melastomataceae (*Topobea*). In *Flora of the Guianas*, A. R. A. Görts-van Rijn, ed. 13:9–21. Koeltz Scientific Books, Königstein.